THE AMERICAN NATURALIST

Vol. XL *February, 1906* No. 470

THE UNITY OF THE GNATHOSTOME TYPE

HOWARD AYERS

Since zoölogists have recognized the simple nature of the Cyclostome fishes there have been many contributions to our knowledge of their structure and many discussions as to their nature and their true zoölogical position.

The increase in our knowledge of the anatomy of amphioxus and the clearing up of its development by the investigations of Kowalevsky, Hatschek, and Willey, have increased the amount of interest in these discussions and have added to the subject an entirely new phase in that the amphioxus, instead of being longer considered a zoölogical curiosity, a degenerated or aberrant form, has become the center of an intense and searching discussion of the origin and relationships of the Vertebrata; and amphioxus has thus come into its own by being recognized as an ancestral form in the genealogy of the vertebrate stock and the oldest living relative and representative of this group of animals.

We can now see clearly enough that the Marsipobranchia and the Acrania both stand in the relation of ancestors to the vertebrates above them, and there is no longer any doubt, while recognizing to the full the many unsolved problems in connection with its structure and development, that amphioxus belongs to the group of forms, the Prospondylia, predecessors of the Archicrania, from which the Cyclostomes are directly descended. It must

be admitted that the gap between amphioxus and Bdellostoma is very great, both as regards time and the amount of the transformation of structure which it has undergone, and that in many things we cannot yet satisfactorily explain the manner in which this transformation has come about.

On the other hand, we may with certainty say nearly as much about the gap between the Cyclostomes and the other Gnathostomes, but the absence of complete knowledge has never been permitted to blind unprejudiced minds to the just estimate of the known facts in any zoölogical problem.

Recent advances in our knowledge of the Marsipobranchs render Haeckel's estimate of the amount of difference between the Cyclostomes and vertebrates above them quite untenable.

He says (*Syst. Phylog.*, vol. 3): "Eine tiefe morphologische Kluft und ein entsprechend langer historischer Zwischenraum trennt beide Classen der Agnathonen nicht bloss von den echten Fischen, sondern auch von allen übrigen Vertebraten die wir in der Hauptgruppe der Amphirhinen oder Gnathostomen zusammenfassen."

There is no reason why we should, at the present time, follow partisans of any genealogical theory of the origin of the vertebrates in ignoring the many anatomical and embryological facts which we now possess and which clearly enough establish the genetic relations of these forms.

Some writers are too prone to assume the existence of large groups of extinct forms intermediate between the groups of existing vertebrates and between these and those forms from which the vertebrates have descended — which have disappeared without leaving any trace of their structure in recent forms.

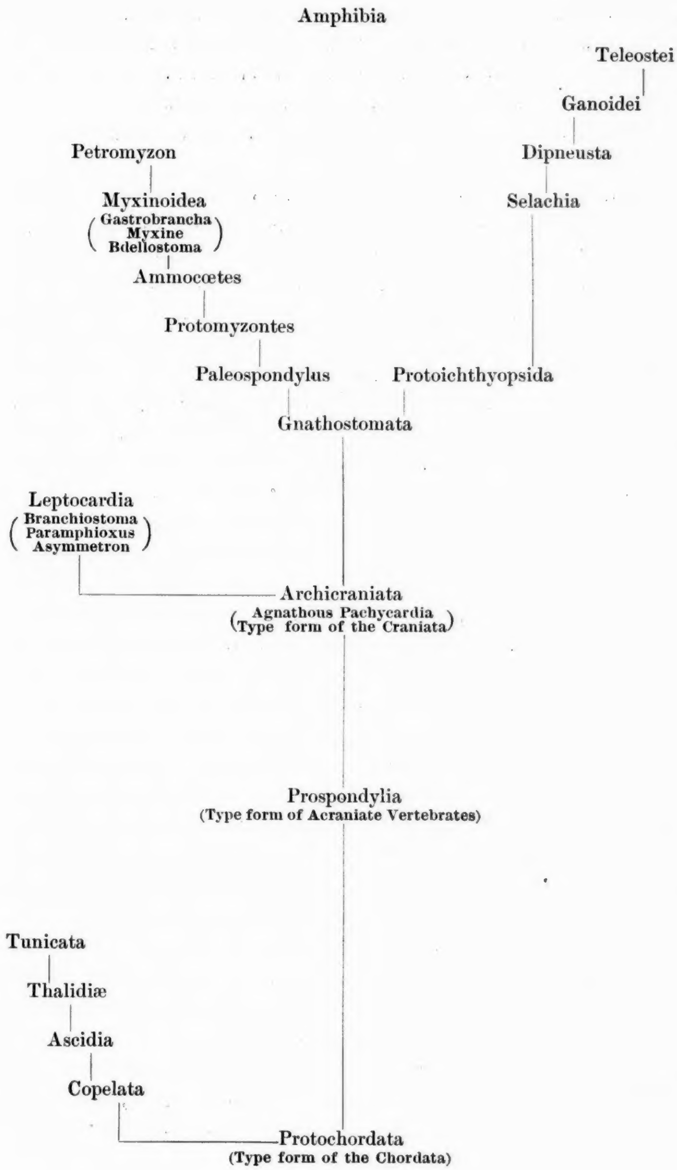
There is neither anatomical nor embryological ground for the removal of amphioxus from the vertebrate class, and we may express our view of the relation of existing forms thus:—

VERTEBRATA

Amphioxus — Leptocardia — Acrania
All others — Pachycardia — Craniata

and by the following table:—

Genealogical Tree of the Ichthyopsida



Before taking up the question of the unity of the Gnathostome type, a brief consideration of some of the general features of the vertebrates will clear the way for a better understanding of the arguments and facts which bear on the solution of the problem.

First of all we may well consider amphioxus as a typical ancestral vertebrate.

The Vertebrata, as we find them to-day, form a morphological unit in much the same way that the birds form a closed group — and it is only through paleontology that the shading off of the group into lower forms is to be found or proven. That the vertebrates have arisen from a common source is a statement which cannot to-day be questioned, for the present state of our knowledge of their anatomy, ontogeny, and physiology is a practical demonstration of the problem. Each increase in our knowledge only makes the demonstration stronger. All three fields of investigation — comparative anatomy, comparative embryology, and paleontology — unite in one affirmation of this fact. All three show that there has been an orderly progression (to use only living forms as examples) from amphioxus to man. No one can read Hasse's *Das natürliche System der Elasmobranchier,* to mention only one of many similar investigations, without having the fact of the historical succession of these early vertebrates indelibly impressed upon his mind. The genetic relationships of this procession of Selachians from the earliest geologic ages, when the fossiliferous records of the vertebrate stock were begun, is proven by the comparative morphologic study of the skeletons of extinct and recent forms and this proof is strengthened by the as yet only partial, embryonic record which has been worked out by many investigators. The course of development is marked by the retention in all living forms of all the divergent branches of vertebrates, from amphioxus up to the mammals, of the same fundamental arrangement of organs and systems of organs, and by the same general cellular structure. The variations in arrangements of the organs and the differences in the histological details of the tissues are not greater than the variations of the external form or of the shape of the internal organs. These are large facts of fundamental value, and have a greater morphologic worth than the many minor variations can possibly have, even when

taken together. They prove the essential unity and genetic relationship of all the Vertebrata.

Semper's view that amphioxus is not a true vertebrate has long since been effectively disproved, and the most forceful part of the proof that amphioxus does belong to the ancestral stock of vertebrates is contained in its simple palingenetic development, at least so far as the earlier stages are concerned.

The method of laying down the gills up to the time that the secondary gills are established, is in every way comparable with the processes of gill formation in Bdellostoma. The transformation of the brain up to the apex of its development is similar to the development of the vertebrate brain, the only difference being that it stops its growth in a very primitive stage of the Craniate brain. The differentiation of the tissues is in every respect the same as that occurring in other vertebrates, except that the process of tissue formation does not go as far, while some tissue systems, which appear in upper vertebrates, are never developed in amphioxus. For example, the masses of connective tissues common to other vertebrates, in the form of true cartilage and bone, are not even hinted at. The statement that its tissues are epithelial is most erroneous.

The lack of formation of such structures as jaws, chambered heart, lacunar hepatic gland, cartilaginous skull, etc., is certainly to be put down as a palingenetic characteristic.

When we seek the type form of the vertebrate stock we are forced to look to the invertebrates as the source of origin. Almost all the groups of the Metazoa have been searched for the ancestral type, and in nearly every case a type-form has been discovered which shows the means of descent sufficiently satisfactory to the individual zoölogist to warrant a long and careful discussion of the manner in which the morphologic and physiologic changes have come about that have resulted in producing the vertebrates as we find them to-day.

Three types of structure have, however, been used more frequently than the others. They are, respectively, nemertean, annelid, and arthropod. All three of these types possess a sufficient number of characteristics in common with the vertebrate type to warrant many parallels being drawn between each of them and the vertebrates.

The great difficulty in the way of accepting any of the well developed jointed invertebrates as the ancestral vertebrate type lies in the necessity of a revolution of the body through an angle of 180 degrees, whereby the dorsal surface of the invertebrate becomes the ventral surface of the vertebrate; and also in the concomitant necessity of the formation of a new mouth and the total disappearance of any trace of the old mouth. While there is, at the present time, abundant evidence to show that the functional mouth of the vertebrate of to-day is a neomorph, and that the original mouth was situated at a point anterior and dorsal to the present location, it does not follow and the evidence does not tend to show, that the old mouth corresponds in any way to the mouth, *e. g.*, of the arthropod.

This translocation of the mouth from the invertebrate ventral to the vertebrate ventral surface must have been connected with the reduction of the circumœsophageal nerve ring, and with the total disappearance of that section of the stomodæum which connects the mesenteron with the mouth by preforating the nervous system through the territory of the circumœsophageal nerve ring.

The fact that the stomodæum no longer perforates the nerve ring is a fact which must be satisfactorily explained by in some way discovering the stages through which the transformation has passed from the invertebrate to the vertebrate condition, or the genealogy of the vertebrate stock with the arthropod as the ancestral form cannot be satisfactorily explained.

There is great doubt that the vertebrates are derived from a highly organized annulate invertebrate. They are more probably a distinct branch split off from the unsegmented worms, and developed independently. Many are the theories which have been offered to harmonize the annulate and the arthropod conditions with the vertebrate, but none of them have accounted for a sufficient number of facts to warrant their general acceptance, and, as above stated, the main difficulty has consisted in the inability to picture the revolution of the invertebrate body in such a way as to make it physiologically possible in living forms.

It matters not what position we take with reference to the origin of the vertebrate stock, when we arrive at the stage of development represented by amphioxus we are compelled to admit, in the light

of our recent knowledge, that amphioxus is a true vertebrate, lacking it may be the first trace of the craniate skeleton, and lacking many of the other features which are characteristic of most of the existing vertebrates, but is nevertheless, the only existing form which serves as a connecting link between the simple ancestral type of structure and the more complex anatomical and physiological conditions of the higher vertebrate.

Some zoölogists have recently re-uttered Semper's opinion, that amphioxus is not a true vertebrate, but such restatement of Semper's opinion is justly to be compared to the restatement of the opinions of the older zoölogists, who at various times held amphioxus to be a worm, a mollusc, and a tunicate. Instead of making assertions as to what amphioxus is or is not, the only scientific method of solving the problem of its actual position in the animal series is by a careful study of its structure and a comparison of this with the structure of the lower vertebrates. Such comparison proves beyond the shadow of a doubt the relation of the amphioxus to the lowest fishes.

A review of some of the salient features of amphioxus' anatomy will not be out of place at this point. As regards the form of the body, all zoölogists recognize the fact that the shape of the vertebrate body is a result of the direct response of the organism to its environment, particularly the necessity of locomotion. The lancet shape of amphioxus is due to its burrowing habit. The lack of paired appendages is due to the fact that amphioxus represents the stage of the development of vertebrate structure when such appendages had not yet been developed. The median fin folds are well developed, both in the head and in the caudal region, and serve the same function in essentially the same way that they do in other vertebrates. There is no trace of a *quasi* lateral fin fold, nor of the buds of lateral appendages in the amphioxus, but neither of these are found in the Cyclostome fishes, which are much more highly organized than amphioxus.

The lack of the development of paired appendages in amphioxus and the Cyclostomes is not a mark of degradation, or degeneration, as some zoölogists would put it, because the whole course of their development and the facts of their morphology prove conclusively that these structures were not called forth by the response

of these animals to the stimuli of their environment in the direction of pedal locomotion on the sea bottom. It is highly probable that these appendages arose as ventrally projecting bar-like structures, to enable the bottom-living forms (since all were bottom dwellers to begin with) to move more readily from place to place on the surface of the sea floor while remaining in contact with the sea floor, thus avoiding the necessity of the more difficult feat of balancing themselves in the lighter ambient fluid above the earth floor, in the effort to effect a change of place.

Paired appendages then *did not arise as fins* for the purpose of *balancing the animal in the water*, but the paired fins of fishes have been developed by the transformation of the primitive paired organs of locomotion, of which the paired appendages of the Amphibia and their descendants are the direct and, in their simplest forms, the least modified derivatives.

When one studies the life habits of amphioxus and Bdellostoma in their natural element and, at the same time, the history of their development, he no longer entertains the idea that these animals have lost paired appendages once possessed by their ancestors, but will, and can only, say that they are the ancestral forms of animals possessing paired appendages, and that in the case of amphioxus and of Bdellostoma we have two stages in the response of the vertebrate stock to the stimulation of the environment looking toward the formation of locomotor appendages.

They are both bottom dwellers of necessity, although they take occasional excursions into the superambient water, but quickly fall back, from the force of gravity, to the bottom. These excursions into the superambient liquid are effected by the motion of the caudal fin from side to side. This fin is the main organ of locomotion used by all fish-like vertebrates for progression through the water.

When amphioxus strikes the bottom after such an excursion, it lies quietly upon its side, since it is unable to coil its body sufficiently to lie on its ventral edge. Most of its life it passes buried in the sand. To enter the sandy bottom in which it lives, it first makes an excursion into the superambient water and then descends head first upon the sandy bottom, boring its way among the particles of sand. When swimming it maintains its body in the dorso-ventral position.

In the case of the Bdellostoma we have a very different condition. The Bdellostoma possesses a body remarkable for its flexibility and its elasticity, and is fitted not only to swim in a dorso-ventral position, but during life, when it rests upon the bottom, always does so with a dorso-ventral orientation. While amphioxus shows a distinct inability to orient itself and maintain equilibrium in this position for any but the shortest periods of time, Bdellostoma exhibits in a high degree the capacity to maintain its position with ease, accuracy, and for an indefinite period. This capacity for the equilibration of its body without the possession of paired appendages is both remarkable and deserving of more careful study than has yet been given.

With the possession of a simple ear, the tubular portion of which lies in one plane of space, and with the lack of equilibrating paddles in the form of pectoral and pelvic appendages, Bdellostoma maintains its position while in motion with at least as great precision and as great apparent ease as any of the vertebrates possessing paired appendages.

It is clear, then, that it is not the necessity for the equilibration of the body that has brought about the development of the paired appendages in the vertebrate stock.

Since the formation of the paired appendages in all other water dwellers besides fishes is for the purpose of moving the body over the bottom, that is locomotion, it becomes very probable that the fish fin is a secondary structure, derived from the primitive pedal appendages, which were used by the ancestral form exclusively for locomotion.

This effectively disproves the theory of Gegenbaur of an ancestral archipterygium, and the Thatcher-Balfour lateral finfold theory, and it removes from the field of vertebrate morphology one of the most difficult problems which it has been called upon to solve, by simplifying the conditions of the problem.

While Bdellostoma is able to swim with ease, accuracy, and precision, and thus change its position in space either for the purpose of capturing prey, avoiding its enemies, or seeking a new position upon the bottom, it is not able to progress upon the bottom except by using the same swimming motion of its caudal region which enables it to progress through the water. It cannot

be said, however, to possess the power of locomotion except by swimming or springing. Undoubtedly the next step in the transformation of the Bdellostoma-like body of the ancestral Gnathostome was the gradual formation of pedal appendages, which enabled it to move easily, certainly, and symmetrically over the bottom.

It is just as erroneous to maintain any hypothesis which would derive the paired appendages of the Amphibia, for example, from the paired fins of fishes as it is to maintain the claim that the pectoral appendages (arms — forelegs) of land vertebrates are derived from the wings of birds.

When we consider the structure of the nervous system we are again brought face to face with the fact that amphioxus represents a developmental stage in the central nervous system repeated by other members of the vertebrate stock. Its nerve cord possesses all the relations to the other main organs of the body that are possessed by the central nervous system of other vertebrates. It lies immediately above the dorsal surface of the notochord in the hollow skeletal tube composed of a connective tissue membrane, in the walls of which, however, no chondroidal tissue is formed, and in which no calcareous matter has at any time been deposited, but this condition of the protective tube of the central nervous system is reproduced in the development of all the other vertebrates, from the amphioxus to man. This tube is not surrounded by skeletal structure in the amphioxus, but it is perforated with lateral openings made through its lateral face for the exit of the nerves passing out from it and entering it. In this it is also in harmony with the conditions found in all other vertebrates.

In the antero-posterior direction, the nerve tube is divided into two main parts, as in all other vertebrates, a brain and a spinal cord. While there are differences of histological value between the spinal cord of amphioxus and higher forms, this difference is hardly greater than exists between species of the higher vertebrates above it.

We may dismiss further consideration of this part of the nervous system with the statement that it is in every respect a vertebrate spinal cord. When we come to consider the structure of the brain, however, we find a simplicity in the arrangement of the

parts, which has until recently been an obstacle to most zoölogists in establishing the homologies between the amphioxus brain and the brain of the Craniata, and even to-day very few anatomists know enough about the structure of amphioxus to be able to establish the homologies which are existent.

Apparently the first zoölogists to note the presence of the amphioxus brain were Leuckart and Pagenstecker, who homologized the entire brain vesicle of amphioxus with four ventricles of the Craniata.

Owsjannikow later held the same view. In 1858, Professor Huxley, after careful examination, decided that the amphioxus neurocœle was the equivalent of the thalamencephalon of the Craniata.

In 1860, Wilhelm Müller concluded that it corresponded with the thalamencephalon and the prosencephalon of the Craniata. He further determined the location of the pigment in the anterior end of the brain tube and found that the pigment granules were located in the anterior ends of the brain cells. He also discovered that the olfactory pit was connected with the anterior end of the brain.

In 1861, Langerhans discovered the true relation of the olfactory epithelium of the olfactory tubercle of the brain. He decided that the amphioxus brain included the whole of the primitive Craniate brain.

In 1891, I described in a brief way some of the anatomical features of the amphioxus, giving the following account of the brain. "The anterior end of the neural axis of amphioxus is a brain and corresponds with a certain definite portion of the brains of other vertebrates. Its anterior wall is the homologue of the lamina terminalis of other vertebrate brains, and the anterior portion of its unpaired ventricle is the thalamocœle."

"I would define the vertebrate brain as follows: the 'vertebrate brain' is that portion of the anterior part of the axial nerve cord, associated with organs of special sense, containing an enlargement of the central canal, which is carried out into all structures formed by the outgrowth of the brain wall. Its walls contain the principal centers for the coördination of sensations and movements. All further additions to this simple brain (amphioxus) are made

in response to the demands of the organs of special sense, with which is associated extension of the coördination apparatus. With such additions we have the compound brain of all other known vertebrates up to man, inclusive."

"Reasons why the anterior end of the nerve cord of Amphioxus is a brain. It is a brain because: —

1. It forms the anterior termination of the neural axis.
2. It stands in intimate relation to the sense organs, eye, and nose.
3. It gives off at least two pairs of sensory nerves provided with peripheral ganglia.
4. It possesses large groups of ganglion cells forming centers of coördination.
5. It possesses an enlarged section of the central canal in the form of an unpaired ventricle with three well marked diverticula — two optic, one olfactory.
6. It is the largest part of the nervous system, at a time when the massive musculature and branchial apparatus of the anterior middle fourth of the body have not reached the stage requiring much enlarged central accommodations.
7. It shows in young larvæ growth to such an extent as to cause a ventral flexure of the chorda, while the brain itself bends downwards and so produces a "cranial flexure."
8. It shows in all other details of structure that *it is not* simply the *anterior end of the spinal cord*, but a *brain*.
9. It shows in a larval stage, soon after the differentiation of fibers in the neural axis (larvæ with one gill slit), a marked differentiation into ganglionic and fibrous regions, and the boundaries of the unpaired ventricle as well as of the lamina terminalis are distinctly marked out. There is then a ventricular segment of the brain reserved for the special sense organs. The fibers appear simultaneously with the formation of the pigment spot, and are in all probability the ways by means of which the sensations from this special sense organ are conveyed backward to the motor centers.
10. Since amphioxus is a vertebrate, these relations *must* have direct and important bearings on the phylogeny of the vertebrate brain and head, and will afford us invaluable aid in clearing up these intricate problems."

"The large collections of ganglion cells just posterior to the thalamocœle are homologous with the medullary nuclei of other vertebrates, since their connections show them to be centers for the control of the branchial apparatus, and the sensory and motor structures lying in the territory of the gill basket, *e. g.*, centers of respiration, deglutition, etc."

"The ontogenetic changes of the neural axis in other vertebrates carry the brain through the condition which in amphioxus remains permanent as the adult brain."

As regards the eye, I announced in 1891 that the eye-spot of amphioxus — that is to say, the unpaired but bilaterally symmetrical patch of epithelial cells lying in the lamina terminalis of the amphioxus brain — is the forerunner of the vertebrate eye, and that, as regards its physiology, it was not a visual organ nor an organ of sight, but an organ for the perception of the variations in the intensity of light.

This pigmented patch of epithelium occupies the same position in the adult amphioxus that the unpaired but bilaterally symmetrical patch of pigmented cells in the embryo sturgeon, as described by Kupffer, and in the embryo of Galeus, as observed by me, does with reference to the lamina terminalis of the brain of these forms.

In both the latter cases the pigmented patch is converted into the recessus opticus, and the recessus opticus gives rise by a process of evagination to the two optic vesicles.

Amphioxus, therefore, presents us with an adult condition which is represented in the higher vertebrate form by the simple condition of the brain wall in the earlier stages of the development of the nervous system.

For a fuller discussion of the anatomical conditions present in the adult amphioxus see my paper (*loc. cit.*, pages 238 to 234).

It is clear from this description of the lamina terminalis in the embryos of the sturgeon and of the dog-fish that the early stage of the eye in fishes is truly comparable, indeed is homologous, with the eye organ in amphioxus and is developed in identically the same way. As I have already pointed out, the pigment in the eye of the amphioxus lies in the inner end of the cells forming the anterior end of the neural tube.

In the sturgeon this pigmented area on the inner face of the

anterior brain wall is subject to the evagination process, being carried out with the cells of the recessus opticus.

My conclusions with reference to the eye of amphioxus were based upon a very extensive study of the eye of both the old and the young of amphioxus, and I was able to show that there is a great diversity in the form of the pigment area in different members of a series of individuals and that there is a tendency for the pigment area to divide symmetrically on either side of the median line.

Of greatest moment, therefore, are my observations and those of Kupffer which show that the pigment to be later used in the retina of the eye is first of all laid down in the inner ends of the cells of a primitively unpaired, even though bilaterally symmetrical, plate of cells which evaginates from the brain as the recessus opticus.

Minot attempts to homologize the vertebrate eye and optic tract with the highly differentiated arthropod eye, supra-esophageal ganglion and the circumesophageal nerve ring, but the idea that the visual organ of the vertebrates is to be sought for in such a specialized organ as the compound eye of arthropods is unsupported by morphological facts.

The nose in amphioxus remains in the form of a conical epithelial pit, whose apex is connected with or is in contact with the anterior end of the brain.

This pit is the so called sinus olfactorius impar, being the remains of the anterior neuropore. The right and left walls of this conical pit are thus morphologically equal, and, notwithstanding the fact that the pit is later pushed to one side by the growth of the base of the median fin-fold, we must hold that it is bilaterally symmetrical both in origin and in adult life and is strictly comparable to the plate of cells which evaginates from the anterior end of the brain of Bdellostoma and of the sturgeon, and which has been conveniently called the unpaired nasal plate.

It has long been accepted that the nasal epithelium of the Gnathostome vertebrate is laid down as a pair of bilaterally symmetrical plates in the embryo and continues paired throughout life, while in the Cyclostome it is laid down in an unpaired condition and ever remains so. Nothing could be more incorrect, for the plate in some Amphibia is identical with that in the Cyclo-

stomes. It is a single patch of cells symmetrically placed with reference to the sagittal plane of the body. In reality it is a double patch, although the indifferent tissue, which later forms a septum, has not at this stage developed.

It is said that in Acipenser embryos a median unpaired nasal plate precedes the paired nasal organ. This being the case, we have all the more reason to consider the Marsipobranch nose a paired structure, even though it appears to develop from an unpaired plate.

There is certainly no truth in Haeckel's dictum that "the pharyngo-nasal canal [of Myxinoids] is a secondary acquirement in connection with parasitic habit."

Notwithstanding that much has been said about the naso-pharyngeal tube of the Myxinoids, the full significance of this structure has not yet been made out. While it at first seemed to be an organ at the height of its development in Bdellostoma, the embryological evidence would indicate that it is a very old structure. We should not forget that in the Petromyzontes it is already closed off from the pharynx, and that in all other vertebrates it arises in a very early stage of embryonic life as a naso-hypophysial invagination of the ectoderm towards the mesenteron. It would thus seem to be on the verge of extinction in the Cyclostomes. No other stages of its development are known to us.

The total absence of an auditory organ in amphioxus is held by certain zoölogists to be a difficulty in the way of accepting this animal as an ancestor of the vertebrate stock.

They point out that in the tunicates, especially in the Appendicularia, there is an otocyst with inclosed otolith, which supposedly serves as an organ for the perception of wave motion in the water. It is also held that, since the tunicates stand in genetic relationship to the vertebrate stock, it is very unlikely that any form intermediate between them and the vertebrates would entirely lack an auditory organ. The error in their reasoning lies in the fact that they assume that the auditory organs of the tunicates and the vertebrates are homologous structures.

This is not the case, as all the evidence, both morphologic and ontogenetic, clearly proves. The vertebrate auditory organ is a neomorph arising within the vertebrate stock, from a sense-

organ rudiment entirely absent, so far as we yet know, from the tunicates. So that the absence of an ear from amphioxus is fully accounted for, at least in so far as relation to the tunicates is concerned. The tunicate ear is, in a strict sense, an otocyst, and not an ear.

With reference to the segmentation of the body of amphioxus, all the evidence seems to point to the ancestral character of this segmentation in relation to mesodermic segmentation of the higher vertebrate forms, with the exception of one peculiarity, which is probably palingenetic in its nature, but which, so far as we know, does not occur unmodified in any other vertebrate. I refer to the origin of the mesodermic segments from two bilaterally placed hollow pouches pushed out from the mesenteron.

From the many indications which have been discovered by numerous investigators, the mesoderm in the higher forms follows this plan of origin, but the architecture of the transformation is cœnogenetically very much shortened and changed, as in the case of many other organs of the body.

There is no occasion to dismiss all the pertinent indications preserved in the higher forms which indicate that this method of origin was the primitive one, simply because complete and well formed diverticula are absent from the ontogeny of the mesoderm in all vertebrates above amphioxus that have yet been investigated.

Regarding the suggested affinity between amphioxus and the annelids in this matter of the segmentation of the mesoderm, the unprejudiced mind will not hesitate to make the conclusion that it is far less intimate than the relationship already described.

The difficulties surrounding the establishment of the homology of the reproductive organs of amphioxus with those of the higher vertebrates are certainly not solved by any reference of the vertebrate stock to the annelids as ancestors, for the difficulty complained of by Minot that the reproductive organs appear segmentally in amphioxus, but non-segmentally in other vertebrates, is only increased by carrying the ancestral vertebrates back to the annelids, for here the segmental arrangement of the gonads is even more primitive and is accompanied by many annelidan characters of the other organs of the body, which carry us farther

than ever away from an explanation of the origin of the internal sexual organs of the vertebrate body. Certainly, when we have to choose between annelids and amphioxus for an ancestor of the vertebrates, it would be giving up much we have already gained to go back to the vermian type when we have an animal such as amphioxus, possessing many of the vertebrate characters already developed and showing a stage of organization which no one can for a moment doubt is immediately below that of the vertebrates and far removed from that of the annelids and tunicates. It is good occasionally for the zoölogist to view in the large and in perspective the whole animal and to take note of the interrelationship of all its parts, together; in other words, to take a "bird's-eye view" of the form being studied in order that minute and occasional differences, which our incomplete knowledge does not yet permit us to explain, shall not be unduly magnified and thereby be given an importance entirely unwarranted, and thus prevent our establishing the homologies and recognizing the real genetic relationships of the form in question. Much that has been said about amphioxus in recent years has been in the nature of zoölogical quibbling, a playing with non-essentials and an ignoring of the fundamental facts of the anatomy and development of this creature.

The intestinal tract of amphioxus also represents an ancestral condition, which is passed through ontogenetically by higher vertebrates. The liver pouch always arises as an unpaired diverticulum of the mesenteron, which later becomes established as a pair of diverticula higher up in the phylum.

As regards the other features of the intestinal tract, they remain in a very primitive condition, and in the Cyclostome we have a decided advance towards the condition occurring in higher forms. In the Cyclostome the liver becomes a massive gland, with the characteristic vertebrate structure, but neither amphioxus nor the Cyclostomes possess a pancreas.

The mouth in amphioxus is extremely primitive and shows no traces of skeletal structures which may yet be safely homologized with the maxillary and mandibular appendages of the Cyclostomes and the vertebrates above them.

The endostyle, which exists in a high state of development in amphioxus and which is well preserved in the larval Ammocœtes,

possesses as its function the collection and transference of food to the pharynx. During the transformation of larval Ammocœtes into the adult Petromyzon the organ is functionless. Beginning with the adult Cyclostome, and from there on throughout the rest of the vertebrate series, its remnant forms the thymus gland.

As regards the excretory organs of amphioxus, the researches of Boveri show that they are segmental in nature and that each tubule opens upon the surface of the body, no collecting duct being formed. Even on the theory of the annelidan origin of the vertebrates this is a stage of development through which the vertebrate ancestors must have passed, and instead of being an argument against the close genetic relationship of amphioxus to the vertebrates above it, it is one of the best examples we have in all zoölogy of the persistence of an extremely primitive condition of an organ, even after the general advancement of the body, in a morphological sense, makes the presence of such segmental organs appear out of place and not in harmony with the stage of development of the organism as a whole.

A similar instance of the persistence of primitive excretory organs in the adult condition is furnished by Bdellostoma, the only vertebrate which possesses a functional pronephros in the adult condition, and when we compare the adult pronephros of the Bdellostoma with the ontogenetic condition of the pronephros as seen in mammals and in birds, we recognize at once that the differences between these two stages are greater than the differences, for example, which we find between the mesodermic segmentation of amphioxus and other vertebrates or the segmentation of the reproductive organs of the same two forms.

So that this evidence, as well as all that I have previously brought to notice, points to amphioxus as the nearest living form among the ancestors of vertebrates.

A glance at the information contained in the table given below will serve as a basis for comparing Bdellostoma with amphioxus, on the one hand, and with the higher vertebrates, on the other.

Table of some of the primitive characters (p.) of Bdellostoma which are embryonic (e.), for higher vertebrates.

1. Notochord. (p. e.)
2. And its extension to the hypophysis. (p. e.)

3. Membranous skeleton of Bdellostoma. (p. e.)
4. Simple heart. (p. e.)
5. Cranial aorta. (p. e.) (Subcordal aorta.)
6. Peritoneo-pericardial cavity. (p. e.)
7. Subintestinal vein. Ventral vein of amphioxus. (p. e.)
8. Passage of subintestinal vein through liver without capillary net (p. e.)
   Persistent subintestinal vein, which passes around portal system.
9. Gill arteries correspond to gill arches, not to hemibranchs. (p.)
10. Vein from pronephros to right cardinal vein. (p. e.)
11. Blood from anterior body walls passes into portal system. (p. e.)
12. Contractile portal heart. (p.)
13. Origin of carotids from lateral branchial commissure. (p. e.)
14. Segmental disposition of somatic and renal artery and veins. (p. e.)
15. Frequent anastomosis between post. card. veins. (p. e.)
16. Inferior jugular veins. (p. e.)
17. Large number of gills up to 14. (p. e.)
    Functional branchial vessels; functional branchial bars or cartilages.
18. Their reduction during ontogenesis. (p. e.)
19. Functional pronephros. (p. e.)
20. Absence of genital ducts. (p. e.)
21. Brain. (p. e.)
22. Cranial and spinal nerves — separation of motor and sensory branches. (p. e.)

When we compare these characters of a Craniate with the conditions obtaining in amphioxus, we find a surprising agreement between them.

I think, from the presentation of facts just made, it is clear that amphioxus belongs to the ancestors of the present day vertebrates. It is, however, neither a Craniate nor a Gnathostome, and it is separated from all the other forms by a zoölogical gap which we cannot yet adequately measure, but which is very large. Let us now pass to a consideration of the relationships of the Craniate Vertebrata.

Let us assume, with Haeckel, that the Prospondylia are the stock from which the Leptocardia and the Archicrania both arose.

From the latter hypothetical group are developed all the Craniate forms which, down to the present time, have been classified in two main divisions: the Cyclostomata and the Gnathostomata.

In 1894, I showed that the so called tongue apparatus of the Cyclostome fishes, particularly of the Myxinoids, was developed by a transformation of the jaw apparatus from the maxillo-mandibular apparatus of some Gnathostome ancestor, and these views, together with the anatomical evidence supporting them, were printed in the *Journal of Morphology*, vol. 17, and in the *Bulletins* of the University of Cincinnati, vol. 1, nos. 1 and 2.

The development of the mouth of Bdellostoma and the pre-oral and postoral bars (the maxillary and mandibular arches) respectively in the early stages of Bdellostoma, before the formation of the tongue apparatus, adds further corroboration of the accuracy of the interpretation of the homologies of the cranio-facial apparatus of the Marsipobranchi.

With the discovery of the jaw apparatus in the Cyclostomes, the most essential character used by systematists for the separation of this group from the Gnathostomes disappears.

Many other characters, however, of which perhaps the absence of paired appendages is the most noteworthy and important, remain as a sufficient ground for a very distinct separation of these forms from the rest of the vertebrates.

But the group Gnathostomata must now include the Marsipobranchi as well as all the forms hitherto included, so that, as our classification now stands, *all* the Craniata are Gnathostomes, and, as before, the only living Acraniate is amphioxus.

The solution of the problem of the origin of the cranio-facial apparatus is thus pushed back upon the extinct vertebrate forms which fill in the gap between the common ancestor of amphioxus and Craniata. Possibly paleontology may bring us the needed information, or it may be that the embryology of some form yet unstudied will disclose the method of the transformation of the acraniate or agnathous into the craniate or gnathostome head.

CINCINNATI, OHIO

OLD AGE IN BRACHIOPODA — A PRELIMINARY STUDY

H. W. SHIMER

The following paper was prepared as the result of studies pursued at Harvard University under the direction of Professor R. T. Jackson, to whose oversight and suggestive criticisms the writer is indebted. Thanks are also due Mr. R. H. Willcomb of Ipswich, Mass., for his kindness in taking the photographs.

In this study we have made use of the fine collection of the Student Paleontological Department of Harvard University, the collections of the Boston Society of Natural History, and those of the Massachusetts Institute of Technology. Unless otherwise stated, the specimens referred to are in the Student Paleontological Laboratory at Harvard University. Those from the Massachusetts Institute of Technology are either still in that institution or have since been transferred to the Boston Society of Natural History.

This paper aims to summarize the principal characters which accompany old age in brachiopods, to illustrate them with some typical examples, and to present a few suggestions as to their origin and meaning.

Following the present usage, we employ the terms, nepionic for the larval or postembryonic stage of an animal's individual development; neanic for the immature or adolescent; ephebic for the mature or adult; and gerontic for the senile or old. Each one of these is further subdivided into three substages by the prefixes, ana-, meta-, and para-, denoting the beginning of a given stage, its culmination, and its decline (Hyatt, '94, pp. 390–397; '93, pp. 93–108).

Senile Characters

Senility is expressed in the shell by one or more, frequently all, of the following characters:—

1. *Lamellosity of Growth Lines.*— The concentric growth lines become more closely spaced and lamellose, with a tendency to pile up at the lateral and anterior borders of the shell.

Examples: a pedicle valve of *Laqueus californicus* Koch, No.

1

1a

FIG. 1.— A senile individual of *Laqueus californicus* Koch from Catalina Island, California. Old age is indicated by the lamellosity of the concentric growth lines on the gerontic portion of the shell and by the change there in the angle of curvature. The resorption of the umbo by the pedicle is likewise shown. No. 715, Harvard.

FIG. 1a.— A different view of the individual seen in Fig. 1, showing resorption of the umbo and of the deltidial plates by the pedicle.

715, up to and including its mature growth, a length of 40 mm., has only one or two strongly marked growth lines, while on its

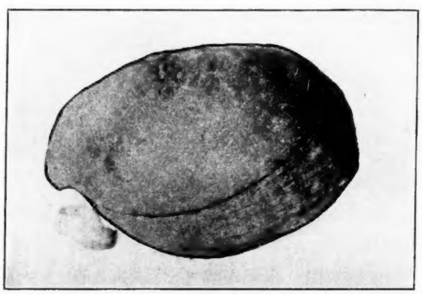
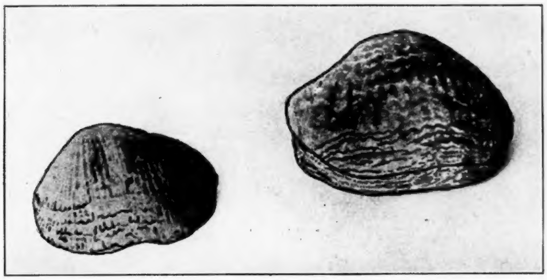


FIG. 2.— A side view of the individual seen in Fig. 1, showing anteriorly the change in the angle of curvature.

gerontic portion there are at least eight in a length of but 10 mm. (Figs. 1 and 2.)

A specimen of *Atrypa spinosa* Hall, No. 499, has in its mature or ephebic stage a length antero-posteriorly of 30 mm. or of 36 mm. measured on the curve of the pedicle valve. In succeeding growth originated a change in the angle of curvature at the anterior portion of the shell, indicating old age (see below). From the umbo up to and including the mature portion of the shell there are 24 well marked growth lines about equidistant; on the gerontic or deflected portion there are nine growth lines in a space of but 4.5 mm. Thus in old age the growth lines become crowded, as one occurs in every 0.5 mm., while in the previous growth one occurred in only every 1.5 mm. The piling up of the growth lines was caused by their continued production unac-



4 3

FIG. 3.— A very large senile individual of *Atrypa spinosa* Hall from the Hamilton of Eighteen Mile Creek, New York, showing the change in the angle of curvature, the groove at the junction of the valves, and the lamellose condition of the growth lines upon the gerontic portion of the shell. No. 499, Harvard.

FIG. 4.— A fully mature individual of *Atrypa spinosa* Hall, on which none of the above gerontic features appear.

companied by any considerable growth of the shell in the anterior direction (Fig. 3).

A Lower Helderberg specimen of *Atrypa reticularis* (Linné), No. 641, shows 12 growth lines on the gerontic portion in less than 5 mm. This is after the abrupt deflection while the preceding portion of about 21 mm. in length also had only 12.

2. *Change in the Angle of Curvature.—This often results in a groove at the junction of the two valves.* An abrupt change in

direction occurs at the lateral and anterior borders of the shell so as to produce maximum growth almost or completely at right angles to the plane of separation of the valves. This change is frequently so great as to produce a reëntrant groove of greater or less depth at the junction of the valves, at the lateral and anterior portions of the shell. The groove results from the failure of each successive growth line to build out as far as the preceding one, and thus results in bending in the edges of the valves so that they meet in a depression.

Examples: in a pedicle valve of *Athyris spiriferoides* (Eaton), No. 498, the first lamellose growth lines appear after the shell has attained a length of 22 mm. and a width of 26 mm. At this period in growth the shell not only ceased to increase in width at the cardinal angles but actually decreased and so produced a groove

5 6

FIG. 5.— *Athyris spiriferoides* (Eaton). A mature individual from the Hamilton group of Eighteen Mile Creek, New York.

FIG. 6.— A senile individual of *Athyris spiriferoides* (Eaton) from the Hamilton of Eighteen Mile Creek, New York. Gerontism is well shown here in the change in the angle of curvature and the conspicuous groove at the junction of the valves. No. 498, Harvard.

1 mm. in depth (Fig. 6). The change in the angle of curvature took place at the anterior portion of the valve later than at the cardinal angles.

In a specimen of *Laqueus californicus*, No. 715, measuring 45 mm. in length by 35 mm. in width, the change in the angle of curvature in old age at the sides of the shell is about 45°, and at the anterior portion is much less. This specimen also shows a shallow, broad groove at the cardinal angles (Figs. 1 and 2).

A slight groove is also developed at the cardinal angles of a

specimen of *Rhynchotrema capax* (Conrad), No. 142, and of *Atrypa spinosa* Hall, No. 499 (Figs. 8 and 3). In these specimens, however, the groove does not extend to the anterior portion of the shell as it does in some.

3. *Rotation of the Umbos toward Each Other.—This results in greater gibbosity of the shell.*

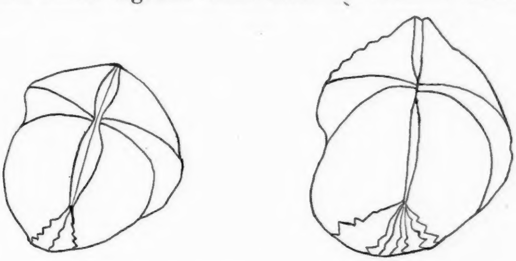
As shown above, the anterior growth of the valves in old age

7 8

FIG. 7.— *Rhynchotrema capax* (Conrad) from the Hudson River group of Cincinnati, Ohio. A mature form.

FIG. 8.— A large senile individual of *Rhynchotrema capax* (Conrad) from the Hudson River group of Cincinnati, Ohio. Senility is shown in the lamellose growth lines and in the extreme gibbosity. No. 142, Harvard.

is at a more or less abrupt angle to the previous growth. This gerontic growth thus tends to push the edges of the ephebic shell farther and farther apart, and causes the valves to rotate outward on the axis of the hinge line. This rotation brings the umbos closer and closer together until often the beak of the brachial



9 10

FIG. 9.— A fully mature form showing in the pronounced growth varices the beginning of senility. *Platystrophia lynx* (Eich.) from the Hudson River group of Cincinnati, Ohio. No. 1910, M. I. T.

FIG. 10.— An advanced gerontic form of *Platystrophia lynx* (Eich.) from the Hudson River group of Cincinnati, Ohio. Old age is especially shown here in the strongly lamellose growth lines and in the closely approximated umbos. No. 1911, M. I. T.

valve encroaches on the delthyrium of the pedicle valve to such an extent as to block the original pedicle opening entirely (Figs.

8 and 10). As long as the pedicle remains active it will resorb the umbo of the pedicle valve as fast as the brachial umbo encroaches upon it, thus keeping a passage open for itself (Fig. 11). From this rotation of the valves there results a lengthening of the dorso-ventral axis of the shell. This gives it a gibbous appearance which is seen even in forms that are in maturity flat and thin, as *Rafinesquina alternata*. This great increase in thickness is shown in Figs. 3, 5, and 6, and also in the following measurements:—

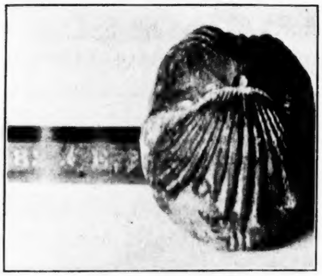
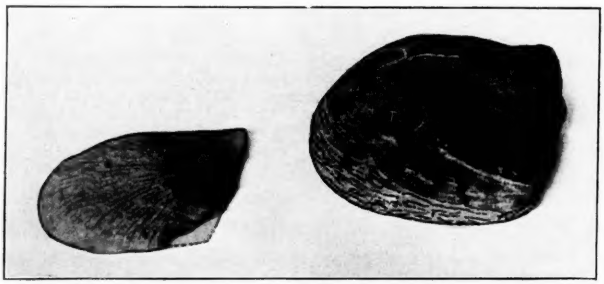


FIG. 11.— *Rhynchotrema capax* (Conrad). Hudson River group of Cincinnati, Ohio. A gerontic individual which has through resorption of the umbo, kept its pedicle passage open *pari passu* with the rotation of the umbos toward each other. No. 1156, Harvard.

Rafinesquina alternata (Figs. 12 and 13). Adult, No. 1912, M. I. T. Length, 32 mm.; breadth, 41 mm.; thickness, 3.5 mm. Old age, No. 128. Length, 39 mm.; breadth, 51 mm.; thickness, 11 mm.

Rhynchotrema capax (Figs. 7 and 8). Adult, No. 1913, M. I. T. Length, 22 mm.; breadth, 21 mm.; thickness, 26 mm.



12 13

FIG. 12.— Mature individual of *Rafinesquina alternata* (Emmons) from the Hudson River group of Cincinnati, Ohio.

FIG. 13.— A large gerontic individual of *Rafinesquina alternata* (Emmons) from the Hudson River group of Cincinnati, Ohio, indicating senility in the lamellosity of the concentric growth lines, in the changed angle of curvature, and in the greater gibbosity of the shell. No. 128, Harvard.

4. *Flattening-out of Plications.*—In old age the plications (ribs) tend to flatten out and disappear. Their presence is usually indicated on the gerontic portion of the shell by zigzag lines of growth, though the surface of the shell is at this area smooth. This is seen in *Rhynchotrema capax, Platystrophia lynx, Tropidoleptus carinatus,* Spirifers, etc., and holds true in all specimens examined (see p. 117).

Examples: in *Rhynchotrema capax,* No. 142, from Cincinnati, Ohio, the pedicle valve has during maturity 15 ribs; during metagerontism it has 11, and at the last growth before the death of the animal there are none, although zigzag growth lines represent them. The brachial valve has during maturity 14 ribs; during metagerontism, 10, with none at the death of the animal.

In *Spirifer oweni,* No. 57, from the Hamilton of Clark Co., Indiana, the ribs become broader and lower until in extreme old age they, as well as the zigzag growth lines at the edge of the shell, have almost entirely disappeared even at the anterior portion of the shell (see p. 117 for further discussion).

The ribs disappear earlier and more completely from the brachial than from the pedicle valve. This was noticed especially in *Terebratella plicata* Say, *Tropidoleptus carinatus* (Conrad), *Meekella striatocostata* (Cox), *Spirifer mucronatus* var. *thedfordense* Shimer and Grabau, and *Rhynchotrema capax* (Conrad). This character is often only faintly marked; its presence is first noted at the cardinal angles. Raymond (:04, p. 128), also notes the more nearly complete obliteration of the plications on the brachial valve in *Tropidoleptus carinatus.*

FIG. 14.—A gerontic individual of *Ambocœlia umbonata* (Conrad) from the Hamilton group of Eighteen Mile Creek, New York, showing the disappearance of the median sinus.

5. *Disappearance of Median Sinus and Fold.* — The median sinus and fold tend to flatten out and disappear in a few observed species.

Examples: in *Ambocœlia umbonata* (Conrad) (Fig. 14), the median sinus disappears in old age. In *Bilobites varicus* (Conrad) there is also a tendency to obliterate the marginal sinus. This is shown in a series of shells, No. 4, from the Lower Helderberg of Clarksville, Albany Co., New York (Fig. 15). For further examples see also Beecher (:01, p. 403).

In some species the median sinus appears to become more accentuated with age. For example, *Athyris spiriferoides* shows well this accentuation of the sinus with hardly any corresponding development of the median fold, while in *Cœlospira grabaui* Shimer, both sinus and fold are developed (Shimer, :04, p. 253).

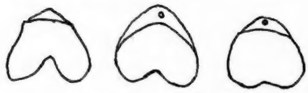


FIG. 15.—Series showing gradual obliteration of the sinus from maturity to old age. *Bilobites varicus* (Conrad) from the Lower Helderberg of Clarksberg, New York. No. 4, Harvard.

6. *Enlargement of Cardinal Angles.*—The cardinal angles, that is, the angles made at the cardinal extremities between the hinge line and the sides of the shell, enlarge during senescence.

Examples: a specimen of *Rafinesquina alternata*, No. 128, has just preceding senescence, a cardinal angle of 87°. This increased to 99° during old age (Fig. 13).

A specimen of *Spirifer mucronatus* var. *thedfordense*, No. 405, has at the close of the neanic or *Spirifer mucronatus* stage (Shimer and, Grabau, :02, p. 171) a cardinal angle of 25°. This angle rapidly increases as seen in Fig. 16, through the ephebic and gerontic stages until it measures 60° at the death of the animal.

7. *Reduction of Shell Index.*—The shell index, *i. e.*, the breadth divided by the length, becomes smaller with old age (see Cumings, :03, p. 3). In other words the shell becomes proportionally longer in old age than in maturity and in this respect approaches the nepionic condition.

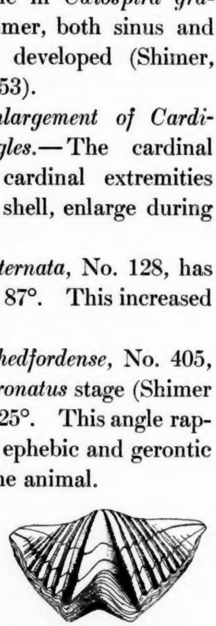


FIG. 16.—A senile form of *Spirifer mucronatus* var. *thedfordense* Shimer and Grabau, from the Hamilgroup of Arkona, Ontario. This shows senility in the enlarging cardinal angles and in the piled-up growth lines. No. 405. Harvard.

Examples: a specimen of *Spirifer mucronatus* var. *thedfordense* has during its nepionic stage a shell index of 1.77; during its neanic, 3.57; and during ephebic, 1.90. For further measurements and discussion of the varietal form see Shimer and Grabau (:02, p. 174).

An old specimen of the above species, No. 405a, had during early maturity a width of 34 mm. and a length of 14 mm., giving a shell index of 2.43. In old age the width was 33 mm., the length 18 mm., and shell index 1.83.

Rhynchotrema capax, No. 142, had in maturity a width of 18 mm., a length of 17 mm., giving a shell index of 1.06. In old age the width was 20 mm., the length 23 mm., and shell index 0.87 mm.

In *Rafinesquina alternata*, No. 128, the mature shell measured 42 mm. in width, 30 mm. in length, and the shell index was 1.40; the senile shell was 51 mm. wide by 39 mm. long with a shell index of 1.30.

8. *Modification of Pedicle Opening.— a. The pedicle opening may be enlarged during growth.* As the animal increases in size the pedicle normally increases in diameter if it continues attached. The resulting growth of the pedicle may resorb the surrounding shell (the deltidium or deltidial plates and umbo) and thus enlarge its opening. This is especially conspicuous in the Terebratuloids. In some shells resorption is made doubly necessary if the pedicle would continue to exist, for the rotation of the umbos toward each other would otherwise soon cut it off. This condition is seen well in some specimens of *Rhynchotrema capax*.

Examples: a specimen of *Laqueus californicus*, No. 715, is a senile individual as indicated by its lamellose growth lines, abrupt deflection, and groove at the cardinal angles. The umbo shows considerable resorption as do also the deltidial plates (Figs. 1 and 1a).

A senile specimen of *Hebertella occidentalis* Hall, No. 2, has a triangular delthyrium 9 mm. high, 5.5 mm. wide at the hinge line, and 2.5 mm. at the apex of the umbo. The delthyrium, already large in maturity with the deltidium resorbed, has been much enlarged in old age; in addition the umbo of the pedicle valve has been resorbed, destroying much more than the nepionic shell (Fig. 17). This destruction of the umbo may be partially due to breaking as shown by an irregularity at the anterior side, but there is no doubt that most of the opening is due to resorption

FIG. 17.— A subgerontic individual of *Hebertella occidentalis* Hall from the Hudson River group of Cincinnati, Ohio, showing the pedicle opening much enlarged through resorption of the umbo. No. 2, Harvard.

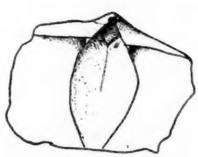
as it has the same general smoothness and evenness of the sides as the delthyrium.

In those forms of *Rhynchotrema capax* which continue attached throughout life, the increasing gibbosity makes necessary, even during late maturity, a resorption of the umbo of the pedicle valve. But this resorption becomes very great in senile specimens, as for example in a specimen, No. 1156, the apex of whose pedicle valve has been resorbed anteriorly at least 1.5 mm. (Fig. 11). The smoothness of this opening and the evenness with which it is prolonged out from the interior of the shell show it to result from true resorption and not from breaking.

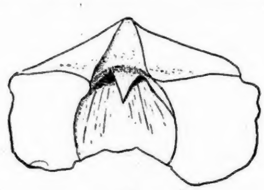
b. The pedicle opening may be partially or completely closed. This is accomplished:—

(1) By deposits of calcareous matter in the apex of the valve, sometimes forming a callosity.

Example: in *Stropheodonta demissa* (Conrad), No. 1914, M. I. T., the delthyrium has been completely closed by growths that extend from either side and meet in the middle; these form two



18



19

FIG. 18.— The interior of the pedicle valve of a mature form of *Spirifer acuminatus* (Conrad) from the Upper Helderberg of the Falls of the Ohio, showing the beginning of the callosity in the pedicle cavity.

FIG. 19.— The interior of a pedicle valve of a gerontic individual of *Spirifer acuminatus* (Conrad) from the Upper Helderberg of the Falls of the Ohio, showing the accentuation of the callosity. No. 646, Harvard.

convex callosities on the inner or proximal side which meet in the median line. The outside of these growths is smooth and also the cardinal margin is wanting in the denticulations characteristic of the rest of the shell.

A testaceous callosity sometimes forms in the pedicle cavity, and extends across the delthyrium (see also Hall and Clarke, '94a, p. 6). This is seen in *Spirifer acuminatus* (Conrad), *S. granulosus* (Conrad), and *S. audaculus* (Conrad).

Example: in a gerontic pedicle valve of *S. acuminatus*, No. 646, the callosity extends 17 mm. from the apex of the valve to the anterior border, uniting the dental lamellæ and sending off a median portion forward between the posterior extremities of the diductor muscle impressions. In a mature valve of this species there appear only faint indications of this callosity in the apex (Figs. 18 and 19). Hall and Clarke ('94a, p. 921), mention this deposit of calcareous matter in the apex of the valve as a frequent condition in senile Spirifers. They also state that "the tendency to contract the pedicle cavity and deltidium presents its extreme manifestations in the Devonian forms of Stropheodonta, Strophonella and Leptostrophia where it has become almost and sometimes quite obliterated and the entire umbonal area filled with testaceous secretions" (Hall and Clarke, '94a, p. 919).

(2) By the encroachment of the umbo of the brachial valve upon the delthyrium of the pedicle valve, so as partially or completely to cover it. This follows from the rotation of the umbos toward each other in senescence as already described (p. 99). When its original opening is thus covered, the pedicle may keep its passage free by resorption into the umbo of the pedicle valve, as already seen (Figs. 1, 11, 17), or may become atrophied and disappear, leaving the shell unattached.

Examples: in a senile specimen of *Platystrophia lynx*, No. 1911, M. I. T., the umbos are so closely appressed that no pedicle opening can be seen (Fig. 10). An approach to this condition is seen in many senile Spirifers, *Rhynchotrema capax*, etc.

9. *Disappearance of Spines, Nodes, etc.*— In old age the surface tends to become smooth, thus repeating the nepionic surface character. In all forms this is noted first at the angles and later at the anterior portion of the shell. There is slight development of surface ornamentation among the brachiopods beyond the simple plications and median sinus and fold. This lack is especially noticeable when we compare this class with the pelecypods, gastropods, and cephalopods which are often characterized by an excessive development of ribs, spines, nodes, etc. If, in brachiopods, spines or nodes are present in maturity, they gradually become less numerous until in extreme old age they disappear entirely (see also Hyatt, '89, p. 20, and Beecher, :01, p. 94). Examples are noted in Productus, Atrypa, and Ambocœlia.

Productus horridus, No. 600, 43 mm. wide and with a length of 82 mm. following the curve of the pedicle valve, has no spines on the last added 12 mm. of the anterior portion, while the spines had disappeared earlier from the surface at the cardinal angles (see p. 110).

Another specimen of the same species, No. 607, has no spines on the last added 18 mm. This disappearance of spines in old age is also well seen in *Ambocœlia spinosa* and in *Atrypa spinosa*. In *Atrypa nodostriata* the disappearance of nodes from the senile portion of the individual was noted.

10. *Thickening of Valves.*— This may result in the formation of an elevated ridge about the muscular area and in the building of a ridge just inside the margin of the concave valve in concavo-convex forms. Both valves, and especially the pedicle valve, thicken by interior additions. The area of maximum increase usually extends from each side of the muscular impression to the cardinal angles. Sometimes, as for example in *Athyris spiriferoides*, the greatest thickening is at the lateral edges of the valves. The pedicle valve becomes especially thickened over the gential organs as seen in Atrypa, Spirifer, etc.

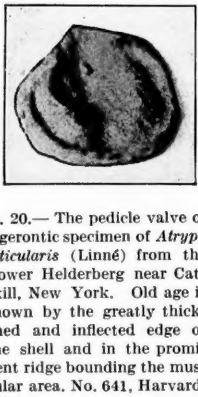


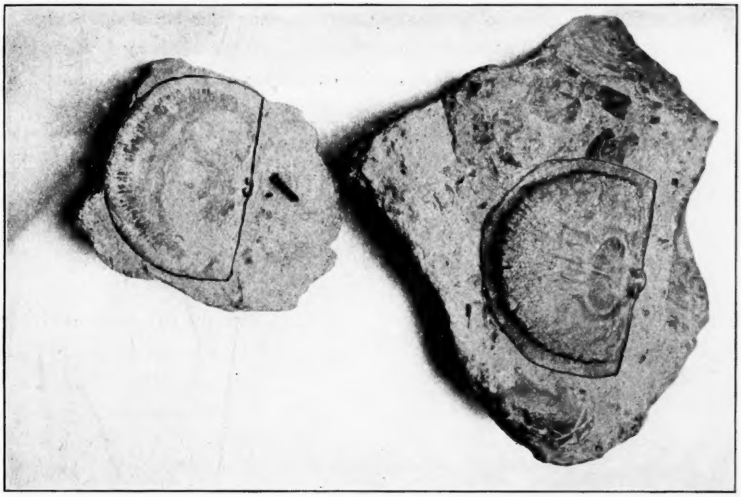
FIG. 20.— The pedicle valve of a gerontic specimen of *Atrypa reticularis* (Linné) from the Lower Helderberg near Catskill, New York. Old age is shown by the greatly thickened and inflected edge of the shell and in the prominent ridge bounding the muscular area. No. 641, Harvard.

Examples: a pedicle valve of *Atrypa reticularis*, No. 641, has a broad, prominent ridge bounding the muscular area laterally and sloping outward to a depression between it and the much thickened and inflected edge of the shell; it disappears entirely anteriorly (Fig. 20).

A pedicle valve of *Spirifer acuminatus*, No. 646, shows a greatly depressed muscular area due to the great thickening of the posterior portion of the valve on each side of it, which slopes gradually to the lateral margins of the valve (Fig. 19).

In *Platystrophia lynx*, No. 3, the pedicle valve is thickened very much at the sides of and anterior to the muscular area (see also Cumings, :03, p. 28).

In the above cases, as well as in all observed, the greatest thickening in the interior of the valve occurs in the region of the principal trunks of the vascular sinuses, and it is in these main trunks that in modern brachiopods the genital organs occur (for further discussion see p. 117). In most concavo-convex and resupinate shells the concave valve bears just inside its margin and posterior to where the convex valve fits over it, a swollen and strongly papil-



21 22

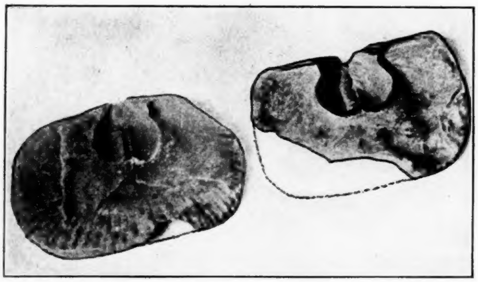
FIG. 21.— A mature brachial valve of *Rafinesquina alternata* (Emmons) from the Hudson River group of Cincinnati. Ohio. No. 1, Harvard.

FIG. 22.— The brachial valve of a gerontic individual of *Rafinesquina alternata* (Emmons) from the Hudson River group of Cincinnati, Ohio, showing the vascular tumid ridge and its abrupt descent to the edge of the valve. Harvard collection.

lose ridge which extends from the cardinal angles to the anterior portion of the shell. In the brachial valve of *Rafinesquina alternata* the ridge has a very irregular surface and descends abruptly to the narrow margin of the valve. This makes the interior of the valve quite flat while the outside is concave (Fig. 22). This submarginal thickening was also noted in *Tropidoleptus carinatus* (Conrad), *Strophomena rugosa* Blainville, *Plectambonites sericeus* (Sowerby), *Chonetes granulifera* Owen, *Stropheodonta magniventra*

Hall, and *S. concava* Hall. Sometimes the papillæ are so well developed that they are spine-like. This was most conspicuous in *Stropheodonta magniventra*, No. 1165, and in *S. concava*, No. 1099, M. I. T.

In the majority of brachiopods the muscular area of the pedicle valve becomes in gerontic individuals depressed below the general interior level of the shell through the thickening of the shell about it, and thus frequently leaves this area translucent in its thinness while the remainder of the shell is very thick. The area is often strongly marked off from the rest of the valve by an elevated ridge at times high and well defined, surrounding it. This ridge is



23 24

FIG. 23.— The pedicle valve of a mature specimen of *Hebertella occidentalis* Hall.
FIG. 24.— The pedicle valve of a gerontic individual of *Hebertella occidentalis* Hall, showing the high ridge defining the muscular area.

conspicuous in *Rafinesquina alternata, Leptæna rhomboidalis, Hebertella occidentalis* (Fig. 24), *Eatonia peculiaris*, and *Hipparionyx proximus*, in all of which the muscular area is strongly marked off from the rest of the shell. In *Spirifer acuminatus* (Fig. 19) the ridge surrounding the muscular area is merged with the general thickening of the shell. We have not been able to examine any senile forms in which the dental lamellæ of the pedicle valve are strongly developed and form a spondylium, as for example in Pentamerus, Gypidula, etc. In these the muscular area is thus raised instead of retaining its youthful position. This thickening of the valves may in a few individuals result in the lessening of the total capacity of the body chamber. Usually,

however, the internal thickening is more than offset by the growth of the margins of the valves toward each other; for even a slight marginal growth means a large increase in the cubic capacity of the shell.

Descriptions of a few Species

The following species were chosen for description of senescence because there were derontic specimens of them in the collections studied and also because they are common. Similar old age characters were, however, noted upon all forms which showed any approach to gerontism. When one specimen is described, this is merely taken as a type but the characters hold true for all the specimens of that species examined.

Rafinesquina alternata (Emmons).— A large specimen, No. 128, from the Hudson River group of Cincinnati, Ohio, was 30 mm. long when it first showed signs of old age in the appearance of lamellosity and in the changed angle of curvature; this change is much more noticeable on the pedicle than on the brachial valve. The shell also increases in thickness from 3.5 mm. in a normal mature specimen to 11 mm. in this gerontic individual. In old-age specimens of this species the pedicle opening is usually entirely closed and if it exists, is much too small to admit the passage of a pedicle large enough to support a shell of such a size (on this point see also Hall and Clarke, '92, p. 141). This condition is not, however, due wholly to senility but existed during maturity.

The interior of the brachial valve has, extending from the cardinal angles around the margin of the valve anteriorly, a tumid ridge with a very irregular surface. This descends abruptly to the edge of the valve. For comparison of mature and gerontic forms see Figs. 21 and 22.

Strophomena rugosa Blainville (*Streptorhynchus planumbonus* Hall).— A pedicle (concave) valve, No. 582, of this species bears just inside its edge a tumid ridge with a considerable vascular surface, which is not developed to such an extent as in the concave (brachial) valve of *Rafinesquina alternata*. This fact is interesting as the ridge is developed in opposite valves in the two species. The muscular area remains translucent while the rest of the valve

becomes much thickened and more or less grooved by vascular markings. Both valves of this species bear lamellose growth lines. There is also a greater lamellosity in the latest built portion of the deltidium and chilidium.

Productus horridus Sowerby.— No. 600 from the Lower Zechstein of Gera, Thuringia, is not very senile. Old age, however, is indicated by the greater concavity of the brachial valve and by the absence of spines from the last added 12 mm. of the anterior portion. They had disappeared before this from the cardinal angles, showing thus the progressive advance of senility from the cardinal angles to the anterior portion. This order of disappearance is just what we should expect from their order of initiation, appearing as they do at the cardinal angles before they develop on the main portion of the shell.

Platystrophia lynx (Eichwald).— A gerontic individual of this species from the Hudson River group of Cincinnati, Ohio, No. 1911, M. I. T., attained a length of 31 mm. before it began to show evidence of old age in any marked degree; after this point it added a length of 13 mm. to each valve. The senescent characters noted here are: lamellosity of growth lines, flattening of the ribs, and formation of a groove at the cardinal angles. Through the change in the angle of curvature and the consequent growing toward each other of the two valves, the entire shell becomes very gibbous. The accentuation of these characters in increasing old age may be seen by comparing Figs. 9 and 10. The cardinal angle measures 78° at the close of the ephebic stage and 94° in the gerontic. Similar observations are given by Cumings (:03, p. 12).

A pedicle valve of this species, No. 3, from the Hudson River group of Cincinnati, Ohio, shows a very pronounced thickening on each side of and anterior to the muscular area. This area thus appears to be very much depressed, with high, perpendicular bounding walls. The development and relationship of this species are very thoroughly discussed and illustrated by Cumings (:03).

Rhynchotrema capax (Conrad).— A specimen of this species, No. 142, from the Hudson River group of Cincinnati, Ohio, after reaching maturity when it had a length of 15 mm., became lamellose at the cardinal angles and the ribs began to flatten out, while the angle of curvature in each valve became relatively greater.

It then lengthened the pedicle valve 8 mm. on the curve of the shell, during ana- and metagerontism. At this point the growth lines become still more lamellose, more of the ribs flatten out, and a sudden increase in the angle of curvature takes place. From this point it added 7 mm. to each valve. There is shown especially on the median sinus and folds of this latest added portion a groove in the center of each rib on account of the changed plane of growth. A shallow groove is formed at the junction of the valves. This is greater at the cardinal angles since it is there first formed and proceeds progressively anteriorly. This groove is due in the anterior portion to the last added two or three growth lines only. The specimen has the pedicle opening entirely filled by the umbo of the brachial valve. Another specimen, however, No. 1156, as large as the preceding and representing a similarly advanced stage of senescence, has a very large pedicle opening. Mature and gerontic forms are shown in Figs. 7 and 8.

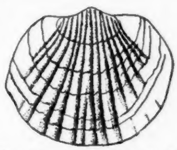


FIG. 25.—A senile individual of *Tropidoleptus carinatus* (Conrad) from the Hamilton group of Eighteen Mile Creek, New York. Old age is indicated in the enlargement of the cardinal angles, reduction of shell index, and in the flattening-out of the ribs. These last always disappear progressively from the cardinal angles to the front of the shell. No. 1915, M. I. T.

Terebratula harlani Morton.—In this species old age is shown in the lamellose concentric growth lines, the change in the angle of curvature, the groove at the cardinal angles, the larger cardinal angle, and the resorption of the umbo and deltidial plates. Exactly similar characters are shown in *T. perovalis* Sowerby.

Tropidoleptus carinatus (Conrad).—In an old-age specimen of this species, No. 1915, M. I. T., the ribs are flattened out on the gerontic portion and the growth lines are lamellose, irregular, and more or less piled up. These senile characters appear progressively from the cardinal angle to the front of the shell (Fig. 25). The cardinal angle enlarges and the shell index grows smaller. The ribs flatten out on the brachial valve before they do on the pedicle valve. In other specimens the submarginal ridge of the concave (brachial) valve, so characteristic of *Rafinesquina alternata*, also occurs, though in a less marked degree. Raymond (:04, pp. 126–131) discusses this species fully.

Laqueus californicus Koch.— A specimen of this recent species, from Catalina Island, California, No. 715, shows old age in the lamellose growth lines, the change in the angle of curvature, and the formation of a groove at the cardinal angles, and in the larger cardinal angles (Figs. 1 and 2). These characters also appear in *L. rubellus* Sowerby, etc.

Atrypa spinosa Hall.— In a specimen from the Hamilton of Eighteen Mile Creek, New York, No. 499, old age is first indicated after a growth of 27 mm. by the sudden crowding together of the growth lines and by the change in the angle of curvature. After this the anterior growth through the change in curvature adds about 5 mm. to the thickness of the shell and 4 mm. to its length measured along the antero-posterior axis. This gives the shell a very gibbous appearance. Senility is first expressed at the cardinal angles as seen in the development there first of the greater lamellosity of the growth lines, the change in the angle of curvature, and the formation of a groove which does not extend far anteriorly. The thickness of the comparatively flat pedicle valve is much greater than that of the brachial. For comparison of the senile characters of this specimen with an adult form, see Figs. 3 and 4. A pedicle valve, No. 641, shows the separation of the muscular area from the rest of the valve by a thick, prominent ridge which is especially developed at its sides, *i. e.*, over the genital organs (Fig. 20). The thickened lateral edges of this form a prominent inflected edge.

Spirifer mucronatus var. *thedfordense* Shimer and Grabau.— A specimen of this species, No. 405, from the Hamilton group of Arkona, Ontario (Fig. 16), shows old age in an increase of the lamellosity of the concentric growth lines, the fading-out of the ribs, the change in the angle of curvature, and the development of a groove cardinally at the junction of the two valves. These characters hold true in all senile specimens of this genus examined. In *S. acuminatus* the greatest thickening of the valves is on each side of the muscular area. This character appears to hold true in all species. In some species (*e. g., euryteines, acuminatus, oweni*, etc.) a conspicuous thickening (callosity) occurs also posterior to the muscular area in the pedicle valve, thus separating it widely from the apex of the valve (Fig. 19).

Nucleospira ventricosa Hall.— Senility in this very small, Lower Helderberg species is shown by a conspicuous roughness or lamellosity of the concentric growth lines in the otherwise smooth shell, a change in the angle of curvature, and the formation of a reëntrant groove at the cardinal angles, the point where senility is first indicated. No shell sufficiently senile to have developed a groove in the anterior portion was observed.

Athyris spiriferoides (Eaton).— One specimen from the Hamilton of Eighteen Mile Creek, New York, No. 498, was 22 mm. long and 26 mm. wide when senescent characters first appeared. After that it grew 10 mm. anteriorly measured on the curve of the shell. This growth increased the antero-posterior axis only 6 mm. The maximum width of the pedicle valve was increased only 2 mm. though the total amount added to the width in old age measured over the curve of the valves, was 11 mm. The rest of the growth both anterior and lateral merely added to the thickness of the shell. In this shell old age is expressed by the lamellosity of the growth lines and the change in the angle of curvature. This latter character is more especially noticed at the sides of the pedicle valve as this valve piled up growth lines here to a thickness of 4.5 mm. The lateral edges of the brachial valve thickened less. A groove was formed at the junction of the valves. The cardinal angle enlarged from 100° in the mature shell to 125° in paragerontism (Fig. 6). This specimen shows the normal progression of old age characters from the cardinal angles to the anterior border, in the first appearance there of the lamellose growth lines and of the groove. This groove at the death of the animal had advanced only halfway to the anterior border of the shell. A separate pedicle valve, No. 635, shows the maximum thickening from each side of the muscular impression to the cardinal angles, with the greatest thickening at the edge of the valve. Figs. 5 and 6 show for comparison a mature and a gerontic individual.

Conclusions.

Minot ('91, p. 151) says very suggestively: "I think it is now conclusively established that there is in guinea pigs a progressive

loss in the power of growth, beginning almost immediately after birth." This same decrease is very realistically shown in the little gastropod, *Litorina littorea*, so abundant on our Atlantic coast. This shell, in the vicinity of Boston, is very quickly attacked by an alga which discolors and erodes it. So if a series of the shells from small to large is collected at mid- or late summer before the new growth has become corroded by the algæ, the amount of that year's growth is very distinctly shown. Such a series shows that, while on the small specimens the year's growth was more than two complete whorls, in older specimens it became progressively less until in some of the mature ones it was but 3.5 mm. Finally on the older shells growth was extremely reduced, being on one shell only 0.75 mm. For these facts concerning Litorina we are indebted to Professor R. T. Jackson whose series of these shells collected from Manchester, Mass., shows the above facts. The series is now on exhibition at the Boston Society of Natural History.

This relative decrease in growth is also shown in the crowding of the septa in old-age cephalopods. Among pelecypods and brachiopods the relative decrease in the amount added to the shell is indicated in the more crowded condition of the later added growth lines. For example, a specimen of *Atrypa reticularis*, No. 641, shows 12 growth lines on the gerontic portion which give a thickness of 5 mm. while the preceding growth, about 22 mm. long, has also only 12. Yet if the growth lines were added at regular time intervals the gerontic stage represented as long a period as that from embryonic through ephebic.

That the more prominent growth lines may define the shell growth for definite periods of time is indicated in the following examples. Buxbaum showed that *Anodonta cellensis*, one of the Unionidæ, had two strongly marked concentric lines and hence three sets of more faintly marked areas, and this shell was known to be three years old (Latter :04, p. 163).

The common oyster commercially marketed is about four years old when gathered. Blue Points, which are smaller, are three years old. This age is broadly indicated on the shells by the stronger growth lines. On the Litorina cited above, the new growth is usually bounded posteriorly by a prominent growth line.

While thus the increase in the size of the animal becomes less and less for each succeeding growth period, a time is reached, varying with each individual, when another factor enters and actual decrease or shrinkage begins. The tendency of the soft parts of animals to contract in old age is familiar to us. (See Hyatt, '96, p. 15; Quain, :03, p. 1478). Through this tendency can be explained many alterations in the hard parts which are otherwise difficult of explanation.

The soft parts and especially the mantle of brachiopods, as well as of molluscs, are so closely related to the shell (Morse, :02,

FIG. 26.— Shell showing gerontic effects produced by injury. *Laqueus californicus* Koch from Catalina Island, California. No. 738, Harvard.

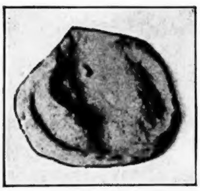
p. 321) that the least change in the former is expressed in the latter. For example, a specimen of *Laqueus californicus* Koch, No. 738, had the anterior portion of the mantle injured. The scars occur in the same relative position on each valve, and the mantle edge left a groove on the shell, indicating the scar (Fig. 26). Before the animal was injured the surface of the shell was very smooth, showing no signs whatever of declining strength, but as soon as the injury occurred a lessened vitality is very noticeable in the change in the angle of curvature and in the lamellose growth lines, simulating senescence.

A change in the angle of curvature of the shell shows that the soft parts of the animal have ceased to grow as fast as formerly. When, however, we consider such gerontic individuals as *Athyris*

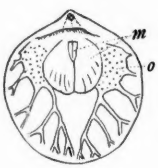
spiriferoides, No. 498 (Fig. 6), and *Atrypa spinosa*, No. 499 (Fig. 3), as described above, it is evident that the growth of the soft parts must have practically ceased, while their secreting activities were continued, but were now almost entirely directed toward thickening the shell (see also Beecher, :01, p. 91).

The formation of a groove at the junction of the valves means further, not only that the growth of the mantle has ceased, but that it is in fact growing smaller, in other words is shrinking. As noted above in the description of *Athyris spiriferoides*, etc., the width of the shell on the right and left axis is less during parageron-tism than it is during the earlier anagerontic stage. This tendency of the soft parts of the animal to shrink and to express this shrinkage in the hard parts is also well exhibited among pelecypods and cephalopods.

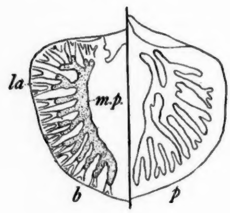
The lamellosity of the growth lines in such types as Athyris,



27



28



29

FIG. 27.— The pedicle valve of a senile individual of *Atrypa reticularis* (Linné) from the Lower Helderberg of Catskill, New York. The prominent ridge surrounding the muscular area occurs beneath the main vascular sinus. No. 641. Harvard.

FIG. 28.— The pedicle valve of *Atrypa reticularis* (Linné) showing the muscular (*m*) and vascular impressions with the ovarian markings (*o*) within the main vascular sinus of the latter. (After Zittel.)

FIG. 29.— Brachial and pedicle half of pallium of the recent *Terebratulina coreanica* with the main pallial sinus and lacunæ filled with eggs. *b*, brachial valve; *p*, pedicle valve; *la*, lacuna; *m. p.*, main pallial sinus (after Morse).

Atrypa, etc., is caused by the relatively decreasing extent of the successive lamellæ of shell growth built in old age. This as resultant brings about a change in the angle of curvature which in extreme cases causes even a resultant angle of less than 90°.

The thickening of the shell on the interior often takes place very irregularly, and leaves the surface strongly papillose. This is well seen in the Spirifers, Stropheodontas, etc. In some Strophe-

odontas, as noted above (section 10), these papillose protuberances become almost spine-like.

The principal thickening in at least many brachiopods occurs over the main trunks of the vascular sinuses (compare Figs. 27, 28, 29; see also Fig. 22). It is a significant fact that in these are located the genitalia (Hancock, '59, p. 817). If a greater contraction took place there it is just in line with what we know occurs in higher animals (Quain, :03, p. 1478). It is usually held that "no gerontic limit is known to the reproductive time in the lower animals" (Hyatt, '97, p. 220). As there is doubtless in most shells an increasing amount of space unoccupied by the soft portion of the animal as it increases in age, it is not necessary to postulate a great shrinkage of the soft tissues to account for the thickening of the shell. Yet the fact remains that in many species the principal thickening is over the main trunks of the vascular sinuses, just where the genitalia occur in modern species and where very probably they were located in fossil ones.

The greater reduction of the lateral growth of the mantle over that of anterior growth in brachiopods is seen in the fact that in old age the shell is proportionally longer than in maturity. The result of these old-age processes appears first at the cardinal angles where the loss of lateral growth to compensate for the shrinkage, causes the flattening-out of the mantle folds (see also Williams, '95, p. 309). The reduction of the radial ribs proceeds progressively from the cardinal angles to the anterior border of the shell and hence it is on the sinus and fold that we find the ribs persisting strongest.

In those cases where the ribs flatten out entirely their continuance is indicated by zigzag lines of growth on the smooth surface of the gerontic portion of the shell. These show that the mantle, after flattening out on one plane, still retained the scalloped border on another. This scalloped edge (as seen for example in *Rhynchotrema capax*) resulted from the faster growing of parts of the mantle over others. As the mantle curved, the parts which formed the summits of the ribs fell behind those which formed the depressions. In other words the portions in the depressions grew faster. This difference in the rate of growth may be seen by following two ribs and their included sinus from the umbo to the front of

the shell, plotting the angles and lengths of the successive growth lines in crossing them (Fig. 30). Thus when the shell surface becomes smooth in old age the zigzag lines of growth where present represent the successive positions of the mantle border. It is as if the plications had been merely transferred from the vertical to the horizontal plane, as the actual mantle is probably scalloped to the same degree in both cases and the absence of ribs results simply from the changed angle of curvature of the shell. Often, hovever, there is a tendency of the mantle edge to fill out the scallops and to present a smooth edge. A beginning in this direction can be seen at the cardinal angles of many plicate individuals. Examples of this are noted in very old specimens of *Spirifer oweni*, *Rhynchotrema capax*, etc.

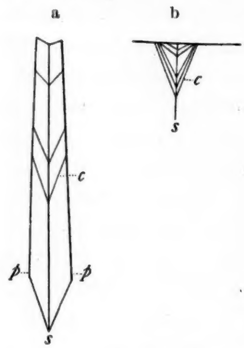


Fig. 30.— Diagrams showing the slower growth of the plications when compared with the furrow between. *a*, enlargement of a furrow and its bounding plications with a few concentric growth lines; *b*, the growth lines of the preceding superimposed on one another, showing graphically the greater growth in the furrow; *p*, plication; *s*, sinus or furrow; *c*, concentric growth lines. These figures were plotted from the median sinus of a specimen of *Rhynchoterma capax*, No. 142, Harvard. × 2½.

The continued anterior growth after the practical cessation of lateral growth causes the cardinal angles to increase in size and causes also the shell index to decrease (see sections 6 and 7). This is a taking-on again of the large cardinal angles and small index of the nepionic stage.

Not only is there repetition of youthful characters in the outline of the shell but there is also a similar repetition in the loss of ornamentation, for the nepionic shell is smooth. An old man with his bald head, curved back, toothless gums, and size smaller than during maturity, resembles the child. Though in these and in many other respects the resemblance is very striking yet in the child the form is the result of positive, developing factors; in the man it is negative, degradational (see also Hyatt, '97, p. 218). So among brachiopods the enlargement of the cardinal angles, reduction of shell index, and the obliteration of ribs, spines, nodes, etc., are in a certain sense a return to the features seen in the nepionic

stage, yet it is a resemblance due to loss of characters. It is thus essentially different from the developing of the similar characters in youth. The characters usually disappear from the shell in the inverse order of their initiation (see also Hyatt, '94, p. 20, and Beecher, :01, p. 269).

As seen above, senility is first shown at the cardinal angles and from there it takes place progressively to the anterior portion of the shell. Hence it is at the cardinal angles that we look for the first expression of old age,— as a change in the angle of curvature, lamellose growth lines, flattening of ribs, and development of a groove at the junction of the valves. Very rarely are individuals found sufficiently old to have expressed on the anterior portion of the shell all of the above senile characters.

When these characters do not appear simultaneously on the shell they appear in a definite order, *viz.*, (1) flattening of ribs, (2) lamellose development of concentric growth lines, (3) change in the angle of curvature, (4) formation of a groove at the junction of the valves, (5) flattening of sinus and fold. This is the usual order, though at the cardinal angles they frequently occur at approximately the same growth line.

Originating thus at the cardinal angles, these gerontic features are pushed farther and farther forward until in paragerontism they are present on the most anterior portion of the shell.

Massachusetts Institute of Technology
Geological Department

LITERATURE

Beecher, C. E.

:01. Studies in Evolution. New York, xxiii + 638 pp., illus.

Beecher, C. E., and Clarke, J. M.

'89. The Development of some Silurian Brachiopoda. *Mem. N. Y. State Mus.*, vol. 1, no. 1, pp. 1–95, pls. 1–8.

Cumings, E. R.

:03. The Morphogenisis of Platystrophia. A Study of the Evolution of a Paleozoic Brachiopod. *Amer. Journ. Sci.*, ser. 4, vol. 15, pp. 1–48, 121–136, figs. 1–25.

Davidson, T.

'86–'88. A Monograph of Recent Brachiopoda. *Trans. Linn. Soc. London, Zool.*, ser. 2, vol. 4, pp. 1–248, pls. 1–30.

Grabau, A. W.

:04. Phylogeny of Fusus and its Allies. *Smithsonian Misc. Coll.*, vol. 44, pp. 1–157, pls. 1–18.

Hall, J., and Clarke, J. M.

'92. An Introduction to the Study of the Brachiopoda. [Part I.] 11*th Ann. Rep. State Geol. for* 1891, *New York*, pp. 133–300, pls. 1–22.

Hall, J., and Clarke, J. M.

'94a. An Introduction to the Study of the Brachiopoda. Part II. 13*th Ann. Rep. State Geol. for* 1893, *New York*, vol. 2, pp. 749–943, pls. 23–54.

Hall, J., and Clarke, J. M.

'94b. Geological Survey of the State of New York. Palæontology. Volume 8. An Introduction to the Study of the Genera of Palæozoic Brachiopoda. Part 2. Albany, xvi + 394 pp., pls. 21–84.

Hancock, A.

'59. On the Organization of the Brachiopoda. *Phil. Trans. Roy. Soc. London*, vol. 148, pp. 791–870.

Huxley, T. H.

'56. Contributions to the Anatomy of the Brachiopoda. *Proc. Roy. Soc. London*, vol. 7, pp. 106–117, 2 figs.

Hyatt, A.

'88. Values in Classification of the Stages of Growth and Decline, with Propositions for a New Nomenclature. *Proc. Boston Soc. Nat. Hist.*, vol. 23, pp. 396–407.

HYATT, A.
'89. Genesis of the Arietidæ. *Bull. Mus. Comp. Zoöl.*, vol. 16, no. 3, xi+238 pp., pls. 1–14, tables.
HYATT, A.
'93. Bioplastology and the Related Branches of Biologic Research. *Proc. Boston Soc. Nat. Hist.*, vol. 26, pp. 59–125.
HYATT, A.
'94. Phylogeny of an Acquired Characteristic. *Proc. Amer. Phil. Soc.*, vol. 32, pp. 349–647, pls. 1–14, 19 text figs.
HYATT, A.
'96. Lost Characteristics. *Amer. Nat.*, vol. 30, pp. 9–17.
HYATT, A.
'97. Cycle in the Life of the Individual (Ontogeny) and in the Evolution of its own Group (Phylogeny). *Proc. Amer. Acad. Arts and Sci.*, vol. 32, pp. 207–244.
JACKSON, R. T.
'90. Phylogeny of the Pelecypoda. The Aviculidæ and their Allies *Mem. Boston Soc. Nat. Hist.*, vol. 4, pp. 277–400, pls. 23–30, text figs. 1–53.
LATTER, O. H.
:04. Natural History of some Common Animals. Cambridge Biol. Series.
MINOT, C. S.
'91. Senescence and Rejuvenation. *Journ. of Physiol.*, vol. 12, 57 pp.
MORSE, E. S.
:02. Observations on Living Brachiopoda. *Mem. Boston Soc. Nat. Hist.*, vol. 5, pp. 313–386, pls. 39–61.
QUAIN, R.
:03. Dictionary of Medicine. 3d ed.
RAYMOND, P. E.
:04. The Tropidoleptus Fauna at Canandaigua Lake, New York. *Ann. Carnegie Mus.*, vol. 3, pp. 79–117.
SCHUCHERT, C.
'97. A Synopsis of American Fossil Brachiopoda including Bibliography and Synonymy. *Bull. U. S. Geol. Surv.*, no. 87, 464 pp.
SHIMER, H. W.
:04. Upper Siluric and Lower Devonic Faunas of Trilobite Mountain, Orange County, New York. *N. Y. State Mus., Rep. N. Y. State Paleontologist for* 1903, pp. 175–269, 4 pls., 10 text figs.
SHIMER, H. W., AND GRABAU, A. W.
:02. Hamilton Group of Thedford, Ontario. *Bull. Geol. Soc. Amer.*, vol. 13, pp. 149–186.
WILLIAMS, H. S.
'95. Geological Biology.
ZITTEL, K. A. VON.
:00. Text-book of Paleontology. Transl. and ed. by C. R. Eastman.

THE HABITS OF *NECTURUS MACULOSUS*[1]

ALBERT C. EYCLESHYMER

NECTURUS although widely distributed throughout eastern and middle North America, is found most abundantly in the rivers tributary to the Great Lakes and in the inland streams and small lakes of the adjoining States. Upon the study of the lake species (*Necturus maculosus* Rafinesque) the following notes are based.

The many names under which Necturus has been described lead to such confusion that some of those most frequently met are here given: *Necturus maculatus, Necturus maculosus, Necturus lateralis, Menobranchus lateralis, Menobranchus tetradactylus, Menobranchus sayi, Menobranchus lacepedii, Menobranchus hyemalis, Phanerobranchus tetradactylus, Phanerobranchus lacepedii, Triton lateralis, Proteus maculatus, Siredon hyemalis, Siren lacertina.* It is known by fishermen and others unacquainted with scientific nomenclature by various names such as: Proteus of the Lakes, Proteus of the Alleghany River, Siren of Barton, mud-puppy, water-dog, water-lizard, fish-lizard, etc.

Size.— According to the writer's observations the adults vary considerably in size, ranging from twelve to eighteen inches. This is based upon an extended series of measurements of individuals taken from different localities and comprising not only the females taken from their nests in the spring, but also both males and females taken in the autumn. It is thus evident that the writer cannot agree with David Starr Jordan ('99, p. 175) and other eminent systematists that Necturus attains a length of 24 inches. In order to ascertain upon what observations these

[1] Rafinesque, in 1818, described this form under the name *Sirena maculosa* (*Amer. Monthly Mag. and Crit. Review*, vol. 4, 1818, p. 41). In 1819, the name *Necturus maculatus* was given (*Journ. de Physique*, vol. 88, 1819, p. 418). In 1820 the specific name *maculosus* was restored (*Annals of Nature or Annual Synopsis of new Genera and Species of Animals, Plants....discovered in North America. First Annual Number*, 1820. Transylvania University, March 1, 1820. Lexington, Ky.).

statements are based, the literature has been carefully searched.

If we turn to the earliest description, given by Schneider (1799, p. 50) we read: "Corpus ultra 8 pollices longum." This measurement was given for the specimen which he found in Hellwig's cabinet at Braunschweig and which Hellwig had obtained from Lake Champlain. The specimen described by Lacépède ('07, p. 230) was obtained by M. Rodrigues and placed in the Natural History Museum but its original source was unknown. The specimen measured 15 cm.

Mitchell ('21) in 1821 received a specimen from Major Delafield taken from Lake St. Clair. In a descriptive letter written to Professor Configliacchi of Pavia we read the following: "He grows, as I am informed, frequently to the length of two feet. The present specimen is not more than one half that length, one of the smaller having been selected for the greater ease of transportation."

A length of two feet is here mentioned for the first time, and as Harlan ('35, p. 164) has already pointed out, this mistake was due to the fact that Necturus and Cryptobranchus were confused by Mitchell. In a letter written to Charles de Schreiber in 1823 Mitchell ('21) even speaks of Necturus as the creature "which the white fishermen have called by the vulgar name of Hell-bender and the Indians Tweeg." It is not difficult to understand how such an error might have occurred since certain naturalists (Daudin Lacépède, Barton) had considered Necturus as the larval form of Cryptobranchus.

Even Cuvier ('29) writes: "L'espèce la plus connue (Menobranchus) vit dans les lacs de l'America septentrionale, et devient fort grande; atteint dit on, deux et trois pieds." Since this time the error has been repeatedly copied.

Coloration.— The color of the adult is so variable that a description does little more than emphasize this fact; indeed the writer has been so forcibly impressed with this variability that it has led to the surmise that Necturus possesses the ability, more or less common to other Amphibia, of changing its color through its control of the black chromatophores. The animal usually appears a dark ashy brown above, with more or less irregular mottling; below it is more evenly colored and of an ashy flesh

tint. The mottling is due to the presence of large irregular dark areas which are surrounded by a pale yellow margin. Often these spots coalesce to form larger areas or bands. In the younger animals there is frequently a dark band extending from the nostril to the eye, from the eye to the anterior margin of the gills, and from the posterior margin of the gills backward along the side of the body. In some cases the upper surface presents no large areas but is more uniform, and the chromatophores and lipochromes are so distributed that the surface presents a granular appearance. The ventral surface of the body frequently becomes lighter toward the median line and in some a sharply defined linea alba is present. The lower part of the head and tail are frequently dotted with small clusters of lipochromes.

In short, the contrast of black and yellow may in some appear vivid, in others subdued and again disappear almost entirely. It is probable that these variations in color are responsible for a number of specific names. As an instance I might state that some years ago Dr. Garnier ('88) described a small Necturus, taken from the Maitland and Lucknow Rivers in Ontario, to which he gave the name *Menobranchus lateralis*, var. *latastei*. "The colouration above was black, the abdomen sooty and the gular fold white."

During the summer of 1904 the writer was fortunate enough to secure two young animals which measured about 4 and 6 inches respectively. The smaller corresponds closely to the description given by Dr. Garnier and there is every reason for believing that the animal in question is the young of *Necturus maculosus*. The older of the two presents the general coloration of the adult. That Necturus should undergo such striking changes in color may appear remarkable to one who has not studied the early stages but when one has followed the changes in color patterns during growth he finds that they are no less striking and remarkable than in the birds.

Habitat.— The environment to which they are best adapted is not known. In spring and summer excepting the time of egg-laying they are most frequently observed in quiet waters from four to eight feet deep where a clean sandy bottom is fairly well covered by vegetation. In the autumn they are found in pairs

or small groups. From this fact and others to be recorded later it is inferred that this is the mating season.

At times they seem to congregate in large numbers. Milner ('74, p. 62) states that "Mr. George Clark of Ecorse, Mich., had a minnow-seine fitted to the bag of a sweep-net, and at one haul took two thousand of the 'water-lizards.' Estimating the extent that the net had passed over, he calculated the average number of 'lizards,' to each square rod, to be four." Milner again states that "a fisherman at Evanston, Ill., a few years ago had nine hundred hooks set in the lake, and in one day took from these five hundred lizards."

Holbrook says that "they are seldom taken except in the months of April and May." Kneeland states that "they are rarely if ever seen except during the winter." The writer has repeatedly taken them through the ice on set lines during the months of January and February. Reese also reports having taken them through the ice in February. While there are no records showing that they are taken in all the winter months there is but little doubt that they are more or less active throughout the winter, a fact which indicates the absence of a period of hibernation.

Necturus moves from place to place at night and rests quietly beneath boards, logs, or stones during the day. In aquaria they avoid the sunlight, and retire if possible to a shaded portion and always seek concealment. Their movement in the water is slow and is effected by walking, in which act the diagonally opposite legs move in unison. When disturbed they move with celerity through a vigorous lateral motion of the broad and powerful tail, with the feet closely applied to the body and motionless. They never swim long distances, at most a few yards, then seek concealment either in the mud or beneath some object.

One is rarely fortunate enough to get a glimpse of them during the day; they seem to be extremely sensitive and disappear at the slightest disturbance of the water, such as that caused by the approach of a boat. If they are undisturbed, one usually sees the head protruding from beneath the concealing object. The animal thus presents a curious appearance with its ruby gills moving gracefully to and fro. When they are disturbed the gills change from their bright red to a dusky color and are at once drawn down tightly against the neck.

When these animals are retained in aquaria they are frequently observed to thrust their snouts above the water, open the mouth widely, and then return to the bottom where they soon expel the air both through the gill slits and from the mouth. It would thus seem that while the branchiæ are the chief means of respiration the lungs play considerable part. Kneeland ('59) made some very interesting observations on this point which are here quoted. "He put two of these reptiles into an aquarium with half a dozen minnows, varying in size from two to three inches. The fish were frequently seen nibbling at the expanded gills of the reptiles, which as often suddenly darted from their ordinary state of repose, attempting to seize the fish, which they never succeeded in doing. In about ten days the menobranchs had nothing left of the gills but the almost bare cartilaginous supports, with only here and there a branchial fringe. The fish were then taken out, and the branchial fringes began to grow again, and in the course of six months had regained about half their normal size. He had watched these reptiles for two summers, and no similar falling of the gills ever took place, so that it appears in the present instance that the fish actually eat them off, their loss being a pathological and not a natural phenomenon. In either case this fact seems interesting from a physiological point of view, as bearing upon the respiratory organs of these reptiles. He had ascertained experimentally that they survive out of water about four hours, showing that their pulmonary sacs, or lungs, are not alone sufficient for the maintenance of respiration. In the present instance, though their pulmonary sacs were the principal respiratory organs, the animals did not apparently suffer....

"The question arises, why are these lungs apparently sufficient for respiration in the water and not in the air, though the respired element be in both cases the same? As there is no evidence of internal gills, the reason must be that in the air the branchial tufts from dryness are unfit for circulating the blood, the complimentary respiration of the skin, so important in reptiles, cannot be carried on — the pulmonary sacs alone are insufficient for the aëration of the blood, and the animal dies. In the water, however, even though the branchiæ, as in this case be useless, the cutaneous respiration is unimpeded and with the pulmonary

is sufficient for the purification of the blood. This fact shows the importance of the cutaneous respiration and the insufficiency of the pulmonary."

Food.— Concerning their natural food little is known beyond the fact that dissections of the alimentary tract reveal the presence of small crustaceans, insect larvæ, and occasionally a small fish. Harlan ('35) and James ('23) both record having found earthworms in the alimentary tract. Kneeland ('58) says: "They seize living worms eagerly and suck them down, if small, with a single sudden swallow; if the worm be large, it is swallowed by repeated suctions, the teeth preventing its escape; the act of suction may be seen by the movements of the impurities in the water, as it is drawn in and afterwards expelled. They often miss the worm; sometimes it may be too far off, but at others so close to them that it seems that their vision must be imperfect. They will not eat a dead worm unless they have been kept without food for a considerable time."

A very curious performance was witnessed by Kneeland and reported by the secretary of the Boston Society of Natural History as follows: "A number of Necturi had been without food for five months when four living minnows were placed in the aquarium, three of the four minnows were swallowed before the expiration of fifteen minutes, and among them the largest. After they had swallowed them, they seemed very uneasy, moving the bones of the head and jaws, and contorting their bodies in various ways, as if they did not feel quite easy in their stomachs; however they at last became quiet, but at the end of twenty hours they became uncommonly active, and the three fish were regurgitated with the scales off, the eyes out, and the entrails of the smallest gone; they were perfectly white, and looked like ghosts of fish. It was either diet to gross for their delicate and weakened stomachs, or else not sufficiently comminuted for the action of their gastric juice." Garnier says that they eat small living fish and crayfish by preference, and do not readily take meat in captivity.

Montgomery states that "from observations of the Menobranchus in an aquarium plentifully stocked with molluscs, such as Physidæ, Limnæans, Paludinæ, Planorbes, Anodonts, etc., as

well as crustaceans I am not warranted in asserting that it feeds on anything other than true fishes."

Milner quotes Clark as stating that "those taken at Ecorse, Mich., were so gorged with white-fish spawn that when they were thrown on shore, hundreds of eggs would fly out of their mouths."

The writer has tried to feed them with various kinds of food. Necturus will readily eat living earthworms but will pay no attention to dead ones. Pieces of liver which are held in forceps and moved gently through the water in close proximity to the snout they seize and devour. But the most satisfactory food is small minnows which at intervals are placed in the aquaria. The movements of the minnows seem to excite the animals whose heads are soon seen protruding from beneath the concealing objects. When the minnow comes in close proximity there is a flash-like movement toward the minnow which in turn either escapes or is swallowed. The writer has observed repeated failures to catch the minnow, but the persistence of the animal is remarkable and it sooner or later succeeds.

From the fact that whenever the water is disturbed in the vicinity of the snout they snap viciously one is led to infer that in taking food they rely almost entirely upon the tactile sense.

Necturus is much dreaded by the ordinary fishermen who regard them as poisonous as do also the Indians (Durkee). According to Gibbes ('53) the negroes are terrified by its presence. He says that "the piggin or wooden vessel, in which an animal was placed after its capture, was destroyed by the negro to whom it belonged, who was resolved never to carry food in it or eat out of it again." Notwithstanding this popular superstition the animal is perfectly harmless and may be handled at pleasure. Its flesh is white and said to be very palatable by Wilder ('74) who writes as follows: "In preparing a paper upon their anatomy and embryology, Dr. W. S. Barnard and myself have had occasion to use them in numbers; and a single fisherman, who sets many hooks for fish has brought us a hundred during the past month (March); he, and all others, apparently regard them as poisonous, and are rather averse to touching them; so far is this from the case, that they are absolutely harmless in every way: and on the 5th Dr. Barnard and myself ate one which was cooked,

and found it excellent: it is our intention to recommend it as food, but not until our investigations are complete."

Their great tenacity of life is a matter of frequent comment. They seem to be able to live for months without food. They have been left for three or four hours out of water and are then easily revived. After severe mutilations they recover, but notwithstanding this great vitality they seem to fall easy victims of a fungus which has not as yet been determined specifically. Mr. Browne (Milner, '74) of Grand Haven, Michigan, states that "some years ago, an epidemic seemed to prevail among the Menobranchi in Grand River, in the month of June, and that their carcasses were washed ashore by hundreds, so that they lined the banks of the river and the mill-men were obliged to throw the bodies off into the current, to be carried down stream to prevent the offensive stench that was wafted into the mills from the decaying remains."

Casting of Epidermis.— Kneeland ('57) states that Necturus sheds its epidermis in the winter. "They shed their skins at this season; I have had several with the old skin hanging to the new in shreds and patches, which are washed off by the water in two or three days, leaving the colors of the new skin very bright; the edges of the tail are then so thin and transparent that the network of blood vessels can be seen with the naked eye."

While endeavoring to obtain a photograph of Necturus on February 9, 1897, Mr. A. H. Cole, one of my students, observed the animal cast its epidermis. His notes read as follows: "The epidermis as a thin layer appeared to have loosened from the entire surface of the body, appearing frosty-white with bubbles of air. The loosened epidermis was split along the mid-dorsal line, its free edges floating upward in ragged streamers. On the following day none of the epidermis remained excepting glove-like portions which were yet attached to the feet; these portions were not cast until two days later."

Breeding Habits.— Although more than a century has elapsed since Necturus became an object of special study on the part of both American and European naturalists, no one seemed fortunate enough to obtain embryological material until Professor

Charles O. Whitman some eighteen years ago discovered the nests and obtained a complete series of developmental stages.

Those who sought the embryological material were forced to enter an unexplored field. No one felt certain that he had even found the adult animal, since the error of Mitchell, that the adult measured two feet, had been and is yet, copied by the leading systematists. Moreover, Barton (Gray, '57, p. 61) held that the animal was the larval form of Cryptobranchus. Cope ('66) expressed the opinion that it was a larval Sperlerpes and changed in the same manner as the Siredon to an Amblystoma. Baird ('50) suggested that it might be the unmetamorphosed form of some great salamander as yet unknown. If the above were true it then remained to be determined whether the animal bred in the larval or the adult condition, or in both. All these possibilities demanded careful consideration.

Again it was not known whether they were purely aquatic or whether they came frequently on land, as described by Smith ('32), DeKay ('42), and others. When this question was answered others arose, and foremost among these was the time of breeding. Concerning this period there were numerous conjectures. Kneeland ('57) states that the animals were taken in abundance near the shore during the winter months. "The reason why they approach the shore at this season may be on account of this change in skin, and possibly for breeding purposes. About once a week they pass from the anus a gelatinous mass, about the size of a pea, of a whitish color, I thought this might be possibly an egg, but the envelope soon becomes soft in water, and its contents are lengthened out into a somewhat convoluted form."

Holbrook ('42) observes that they are "seldom taken except in the months of April and May which is their spawning season. Their eggs are about the size of peas and as many as one hundred and fifty have been counted in a single female."

Milner ('74) states that a "full series was this season ('73) collected from the Detroit River, from the length of one and one fourth inches to thirteen inches. Later, about the middle of the month of July, Mr. George Clark collected a quantity of their eggs, proving this month to be the spawning season of the animal."

Spring, summer, and winter were each regarded as the breeding season and, so far as the observations were concerned, with equal degrees of probability.

Thus there was little to be gathered from the observations previously made. The only reliable data were to be obtained through a systematic examination of the ovarian eggs at different seasons of the year. Even when this tedious work had been carried out and clews obtained as to the egg-laying period, other and greater difficulties arose. The Great Lakes and their tributary streams in which Necturus had been reported most abundant were usually so clouded by muddy water that search for eggs was futile. Localities must be found where the animals were plentiful and where the water remained clear. The small inland lakes of eastern Wisconsin seemed best to fulfil these conditions. Again, no one knew or had even suggested where the animals deposited their eggs, whether in deep or shallow water, whether they were laid in masses in open places like those of Amblystoma, or scattered in strings like those of the toad, or laid singly and concealed among the leaves and branches of aquatic plants like those of the newt.

The knowledge of the egg-laying habits of other Amphibia gave no clue, but nevertheless the work was continued and after years of persistent and patient effort Professor Whitman finally discovered the nests and eggs of Necturus. Only those who have for years been baffled in their attempts to obtain the embryological material of other North American Urodeles, such as the Siren, Amphiuma, and Cryptobranchus can properly appreciate the enormity of the task.

Through the kindness of Professor Whitman the writer first obtained a knowledge of the habits and breeding places of Necturus, and each summer for the past eight years has made observations on the habits of these animals in their natural environment.

Egg-laying.—The time of egg-laying varies in different lakes, depending upon the time when the temperature of the water reaches a certain degree. In the larger, deeper lakes with bold shores this is much later than in those possessing wide shoals. Again, in the individual lakes the time is dependent upon the same conditions. The eggs are first deposited in those localities where the water is shallow and exposed for the greater part of the day

to the sun. The period of egg-laying usually covers two or three weeks. There is no foundation whatever for the statement made by Hans Virchow[1] that the animals deposit their eggs so to speak at the same hour.

According to Professor Whitman's and my own experience the best time for collecting is during the middle and latter parts of the month of May. The writer has collected eggs as early as May 3, and as late as June 5, but these extremes mark the beginning and closing of the early and late seasons.

Preparatory to egg-laying, Necturus seeks the sandy shoals of the lakes or streams. They seem to prefer those localities where the bottom is strewn with numerous logs and boards. It is more than probable that the animals seek these grounds at night since they are rarely if ever seen moving about during the day.

During the day they lie quietly concealed beneath the various objects and one not familiar with their habits would rarely if ever detect their presence. If one desires to see the animals in their natural positions he must approach with much care and he may perchance be rewarded by seeing the head of one protruding. If, however, the jar of the boat or the scraping of an oar has caused them to hide, he must overturn the concealing object. If this is done with great care the animal is occasionally undisturbed and lies for some time motionless, then begins to crawl slowly about. If, however, the disturbance be violent it darts away and conceals itself beneath some other object.

The nest of Necturus, if indeed, such it may be called, is, as has been said, always carefully concealed beneath some object and consists of nothing more than a slight excavation in the sand with a narrow opening through which the animal's head protrudes; the nest is thus perfectly guarded against the attacks of enemies. The objects beneath which the nests are most frequently found are clean logs or boards which lie partially imbedded in

[1] *Sitzb. Ges. naturf. Freunde zu Berlin*, 1894, p. 37: "Necturus kommt in den zalreichen Seeen im südlichen Wisconsin häufig vor und auch an anderen Stellen der Vereinigten Staaten. Die Laichzeit ist nach mündlichen Angaben der Brüder Meyer Mitte Mai, im Jahre 1893 fiel sie auf den 22. Mai, d. h. später wie gewöhnlich; sie variirt nach dem Wasserstande. Die Thiere legen nicht zu verschiedenen Zeiten ab, sondern angeblich zu gleicher Zeit, sozusagen auf dieselbe Stunde."

the sand. The writer has also found them beneath pieces of tin, canvas, and even an old hat.

The depth of the water in which these nests are found, is variable. The writer has found nests covered by only four inches of water, again a nest was found beneath a board at a depth of ten feet, but these are unusual conditions. The majority of nests are found at a depth of from two to four feet. The nests are often found in close proximity to one another; and it is not at all exceptional to find several nests on a single board frequently not more than a foot or two apart. In one instance ten nests were taken from a single board not more than twelve feet long.

In order to facilitate the collection of eggs it has been found advantageous to place boards in suitable localities during the early spring months. When the breeding time has come many of these shelters will have been chosen as nesting places.

During egg-laying the males are never found with the females, and where they remain is unknown. In just what manner the female deposits the eggs is also problematic. There are different stories told by those who during recent years have acquired some knowledge of their habits. In some way the female brings her body in such a position that the eggs are deposited on the sheltering object. When the laying is finished the eggs are found scattered over a surface from six to twelve inches in diameter. The eggs are attached singly by the outermost of the three enclosing envelopes and are about a quarter of an inch in diameter, of a pale cream-color, sometimes showing a faint tinge of green.

The period of deposition undoubtedly covers many hours and probably in some instances, days, since in several cases all the eggs were removed from nests and the following day freshly deposited eggs were found. Further proof is found in that the same nests frequently contain eggs in both early and late cleavage stages. This supposition is further confirmed by the fact that some days after the beginning of egg-laying the oviducts yet contain mature eggs.

If one wishes to leave the nest in such a condition that the female will return and continue laying he must exercise great care in replacing the object to which the eggs are attached. If the nest be much disturbed, one will find upon his return for a fresh

supply of eggs, that even those which were left are missing. Several times the writer has found an animal in the nest whose stomach was distended with eggs. The inference, although positive proof is wanting, is that the parent devours her eggs when the nest is much disturbed.

The length of time which intervenes between deposition and the beginning of cleavage has been accurately determined in a single instance in which four eggs were deposited after the animal was placed in the aquarium. These were placed in a hatching dish in which the water was 17° C. In one egg the first cleavage groove appeared in 18 hours, in two at 20 hours, and in one at 23 hours. The time in some cases certainly exceeds 24 hours, since eggs taken from the nest were kept in a hatching dish for this length of time before cleavage began.

LITERATURE

Baird, S. F.

'50. Revision of North American Tailed Batrachia, with Descriptions of New Genera and Species. *Journ. Acad. Nat. Sci. Phila*, ser. 2, vol. 1, pp. 281–294.

Cope, E. D.

'66. On the Structures and Distribution of the Genera of the Arciferous Anura. *Journ. Acad. Nat. Sci. Phila.*, ser. 2, vol. 6, pp. 67–112, pl. 25.

Cuvier, G.

'29. Le regne animale. Paris, new ed., vol. 2.

DeKay, J.

'42. Natural History of New York. Part 3. Albany.

Garnier, J. H.

'88. [On a New Species of *Menobranchus* (*lateralis* var. *latastei*).] *Proc. Can. Inst.*, ser. 3, vol. 5, pp. 218–219.

Gibbes, L. R.

'53. Description (with Figure) of *Menobranchus punctatus*. *Boston Journ. Nat. Hist.*, vol. 6, pp. 369–373, pl. 13.

Gray, J. E.
'57. On the Genus Necturus or Menobranchus, with an account of its Skull and Teeth. *Proc. Zool. Soc. London,* vol. 25, pp. 61–64.

Harlan, R.
'35. Medical and Physical Researches or Original Memoirs. Philadelphia.

Holbrook, J. E.
'42. North American Herpetology; a Description of the Reptiles inhabiting the United States. Philadelphia, 4to, 5 vols., illus.

James, E.
'23. Account of an Expedition from Pittsburg to the Rocky Mountains, 1819–20. London, 3 vols.

Jordan, D. S.
'99. Manual of Vertebrates of the Northern United States. Chicago, 8th ed.

Kneeland, S.
'57. [On a supposed New Species of Siredon.] *Proc. Boston Soc. Nat. Hist.,* vol. 6, pp. 152–154.

Kneeland, S.
'58. [Habits of Menobranchus.] *Proc. Boston Soc. Nat. Hist.,* vol. 6, pp. 371–373.

Kneeland, S.
'59. [On the Breathing Apparatus of the Menobranchus.] *Proc. Boston Soc. Nat. Hist.,* vol. 6, pp. 428–430.

Lacépède, B. G.
'07. Sur une espèce de quadrupède ovipare non encore décrite. *Ann. Mus. Hist. Nat. Paris,* vol. 10, pp. 230–233, 1 pl.

Milner, J. W.
'74. Report on the Fisheries of the Great Lakes: the Result of Inquiries prosecuted in 1871 and 1872. *Report U. S. Fish Comm.,* 1872–73, pp. 1–75.

Mitchell, S. L.
'21. Observations on Several Reptiles of North America, which seem to belong to the Family of Proteus, etc. *Amer. Journ. Arts and Sci.,* vol. 7, pp. 63–69.

Schneider, J. G.
1799. Historiæ Amphibiorum Naturalis et Litterariæ. Jena.

Smith, J.
'32. [Necturus coming out on Land.] *Isis,* p. 1088.

Wilder, B. G.
'74. Menobranchus Edible. *Amer. Nat.,* vol. 8, p. 438.

NOTES AND LITERATURE.

ZOÖLOGY.

Kellogg's American Insects.[1]— It is gratifying to observe the great progress that is being made in the science of entomology, and to welcome a book such as the author now brings before the public. While the biological side is strongly emphasized it is not overdone and we have the subject presented in a much broader sense than has perhaps ever been done in a single volume. It is written in a clear and popular style, and the fact that the species of economic importance are more fully treated adds much towards making the work of general interest. The 674 pages are illustrated by over 800 figures in the text and 18 colored plates, well selected to show the biologic, systematic, and economic features in the study of insect life.

The first chapter treats of the structure and special physiology of insects, and the second of the development and metamorphosis, followed by the classification and description of the various groups arranged under 19 orders, with keys to the families and many of the genera.

The student will naturally compare this work with that concise and well balanced volume, Comstock's *Manual*,— a work dearer to the hearts of American entomologists to-day than a year or two after its publication. While the new work is quite different in its general makeup, and of a more popular nature, it has not been edited with as much care, but, considering the size of the volume there are comparatively few mistakes, and those which might be misleading to the young student can be briefly noted as follows: on page 201 the figure of *Ranatra fusca* represents either an imperfect specimen, without wings, or an immature example; the respiratory tube is also poorly shown; Fig. 317 is a Micromus not Hemerobius; *Coptocycla aurichalcea*, Fig. 389, and *Cassida bicolor* mentioned in the text (page 281) are synonymous (the latter specific name is now used); Fig.

[1] Kellogg, Vernon L. *American Insects.* New York, Henry Holt and Co., 1905. 8vo, vii + 674 pp., 13 pls., 812 text figs. $5.00.

463 is *Dasyllis sacrator*; Fig. 500 is *Sepedon fuscipennis* not *fascipennis*; Plate 12, Fig. 3, is *Synchloë reakirtii* not *genutia*; Plate 13, Fig. 3 is an *Elis* sp.; Figs. 681 and 682 undoubtedly represent the same species. Although questioned, it is hard to account for Fig. 684, which belongs to an entirely different family; the male of *Pelecinus polyturator* is figured in Packard's *Guide to the Study of Insects*.

Following the chapters devoted to the descriptions of the various orders is a very interesting chapter on insects and flowers in which the pollination of various plants by insects is described. A chapter on "Color and Pattern and their Uses" presents a subject open to much criticism. There is a tendency to carry the so called "mimicry," or preferably protective resemblance, beyond the limits of our everyday walks in the fields and woods, *i. e.*, to emphasize this feature by selecting the most pronounced forms from the fauna of the world and arranging them in museums regardless of their natural surroundings. The "dead-leaf butterfly" (Kallima) is very effective arranged on a twig among the dried leaves of the elm or beech, but when we read that the butterfly usually alights on the trunk of the tree head downward, the charm is broken. Our various species of Polygonia (Grapta) and several groups of moths present fully as interesting examples of protective resemblance. A very instructive and timely chapter is devoted to insects and disease. The work concludes with an appendix on collecting and rearing insects.

C. W. J.

Kingsley's Elements of Comparative Zoölogy.[1]— In this second edition of Kingsley's *Elements of Comparative Zoölogy* the most marked changes from the first edition (1897) are due to a rearrangement, the descriptive part being separated from the laboratory directions and brought together to form the last two thirds of the book, under the heading, in the table of contents, of "Systematic Zoölogy." This plan, which is that adopted by the same author in his *Comparative Zoölogy of Vertebrates*, would seem to be of distinct pedagogical value owing to the confusion in the student's mind arising from the discontinuity of the other arrangement. The questions for a tabular comparison of the forms studied and the groups to which they belong — an especially valuable feature — have been retained, and in a few cases somewhat extended. On page 108 there is a repetition of questions (3 and 7) which should be corrected.

L. J. C.

[1]Kingsley, J. S. *Elements of Comparative Zoölogy*. Second edition, revised. New York, Henry Holt and Co., 1904. 8vo, x + 437 pp.

Punnett's Mendelism.[1]— A useful popular exposition of Mendel's law of heredity. It contains a brief biographical sketch of Gregor Mendel, an account of his experiments in hybridizing plants, the rediscovery of his law of heredity long after Mendel's death, with numerous examples of Mendelian inheritance in animals as well as in plants. No complete account is given of the development of Mendelian theory since 1900, nor does the book contain a bibliography.

W. E. C.

Hantzsch's Birds of Iceland.[2]— This substantial contribution to faunal ornithology is a good example of the present-day "local list," or *résumé* of the avifauna of a circumscribed area. Iceland, because of its position and physical features, affords an unusually interesting field for study. The grass-lands, the moors, the barren mountain tops, the glaciers, rivers, woods, and sea here provide a variety of country, but the rigorous environment is unsuited to many land birds.

The author in his introduction, summarizes briefly the ornithological literature of Iceland, and at the end of the chapter lists the more important works dealing with Icelandic birds. The topography of the island is then treated and the species peculiar to the different areas are listed. An interesting feature is the hot springs which never freeze in the winter and make it possible for certain species to pass the cold season in their vicinity far to the north of their usual winter range.

A number of changes in the avifauna within historic times are noted. Certain birds of prey have evidently decreased, as have also certain fresh-water ducks. Eider ducks, owing to recent protective legislation are more abundant now than formerly. The cliff-breeding Alcidæ are for the most part holding their own. The Great Auk was exterminated in Iceland in 1844. Following chapters deal with the derivation of the birds of the region, their migrations, and their economic importance to the Icelandic people. The migrations are of particular interest and might well have been treated in more detail. A number of wanderers reach Iceland during the fall migrations,

[1] Punnett, R. C. *Mendelism.* Macmillan and Co., London, 1905. 16mo, vii + 63 pp.

[2] Hantzsch, Bernhard. *Beitrag zur Kenntnis der Vogelwelt Islands.* Berlin, R. Friedländer and Sohn, 1905. 8vo, vi + 341 pp., 26 figs., 1 map. 12 Marks.

having evidently been blown out to sea by southerly storms in crossing from Norway to the lands to the south. Migrants to the far north and Greenland pass through on their migrations, or come down in fall to winter, for the warm Gulf Stream waters keep the southern coast of Iceland largely open in the cold months. The fall migration of native birds is chiefly to the southeast, *via* the Faröe Islands to the British Isles or to southern Norway, and the reverse in spring.

The second part of the book is devoted to the annotated list of Icelandic birds, with synonymy, and notes on the habits. One hundred and twenty species are recorded as certainly known, exclusive of the Great Auk. The greater part of these are water birds, and some thirty-two only are land birds, of which latter, but twelve are known to breed in Iceland. In the notes relative to the different species is brought together a great mass of valuable information largely the result of the author's personal experience. A few of the more interesting notes are the account of the nesting of *Megalestris skua*; the occurrence of a single specimen of the Yellow-nosed Albatros (*Thalassogeron chlororhynchus*) for several seasons on the south coast until shot (in 1846); the nesting habits of Barrow's Golden-eye Duck; and the occurrence of such American species as the American Widgeon, Belted Kingfisher, the Lapland Longspur (rarely noted with flocks of Snow Buntings).

The author's use of Latin names differs somewhat from the accepted usage of American ornithologists. Thus the Kittiwake is *Rissa rissa;* Palidna is used as an emendation of Pelidna. We are glad to note, however, that the Ringed Murre is not considered a distinct species from *Uria troile.*

G. M. A.

Holder's Half Hours with the Lower Animals.[1]— Dr. Holder, to use his own rather awkward phraseology, has "endeavored to make this volume a popular combined review and supplemental reader on the lower forms of animal life from the Amœba to the insects inclusive." There are twenty-nine chapters, twelve of which are devoted to the different families of insects, four to crustaceans, and one each to most of the other groups. It seems to the present reviewer a mistake to have attempted the combination of text-book and reader. The result is neither fish, flesh, nor fowl. There is

[1] Holder, Charles F. *Half Hours with the Lower Animals. Protozoans, Sponges, Corals, Shells, Insects and Crustaceans.* New York, American Book Company, 1905. 8vo, 236 pp., illus.

a great deal of information about the more interesting species, enlivened by bits of personal observation on the Florida reefs and off the California coast. Every now and then the author remembers that the book was also intended for a text-book, and injects accounts of the external or internal anatomy of the group or species under discussion with references to accompanying figures. There is constant evidence either of careless throwing together of notes or of a very poor literary handling of material. On page 81 the reader has been hearing about Lingula for nearly two pages, when suddenly in the very midst of a paragraph he takes a flying leap into a Sikh rebellion in India and is put to flight by a horde of land leeches which drop from the trees. On page 213, the author, speaking of butterflies, refers to a figure of the head of a moth; moreover the figure shows the pollinia of an orchid attached to the moth's eyes, and the reader is allowed to assume that they are a structural part of the head.

The book has decided merit as a reference book or a supplementary reader for a class in nature study. If the author had not coquetted with the text-book idea, and had arranged his material with more care, the book could have been greatly improved. The illustrations are excellent.

R. H.

Notes.—*Additional Records for New England Crustacea.* Since the publication of Miss Rathbun's list of the New England Crustacea (*Occasional Papers Boston Soc. Nat. Hist.*, vol. 7, no. 5, July, 1905) the writer has gone over the study series of the Society's collection and the more recent acquisitions. During this work notes were made when the specimens found added something to the records published in that list, either in the way of localities, extension of range, or the animals with which the crustacean was associated either as a parasite or in a symbiotic relation. These records follow:—

Uca minax (LeConte).— Above Fall River, on the Taunton River, were found all three species of Uca; on sandy flats on the outer river bank were found *U. pugnax* (Smith) common, and *U. pugilator* (Bosc.) a few. In Thatch Pond, a somewhat protected area, were found *U. pugnax*, a few, and *U. minax* (LeConte) very plentifully.

Sesarma reticulatum (Say).— A single specimen of a male from Bristol, R. I., and several specimens from Wood's Hole, Mass.

Pinnotheres maculatus Say.— Specimens from gills of *Modiolus modiolus* Linné, Vineyard Sound.

Pagurus pollicaris Say.— A single specimen from Beverly Bridge, Mass., collected by J. H. Emerton, gives a northward extension to the range of this species.

Cirolana polita (Stimpson).— Specimens from Ipswich, Mass.

Æga psora (Linné).— Single specimens from Head Harbor, Me., Matinicus Island, Me., and off Thatcher's Island, Mass.

Nerocila munda Harger.— Specimens from fins of file fish, Buzzards Bay, Mass.

Chiridotea cæca (Say).— Eastport, Me.

Asellus communis Say.— Salem (J. S. Kingsley, coll.) and Boston, Mass. (S. Henshaw, coll.).

Tryphosa pinguis (Bœck).— Eastport, Me., (A. S. Packard, coll.).

Ampelisca macrocephala Lilljeborg.— Specimens from Grand Manan give a more northern record. There are also specimens from No Man's Land, Mass. (A. Hyatt, coll.).

Ampelisca compressa Holmes.— Also from No Man's Land, Mass.

Byblis gaimardii (Kröyer).— Eastport, Me.

Haploöps robusta G. O. Sars.— Massachusetts (H. B. Storer, coll.).

Acanthazone cuspidata (Lepechin).— Eastport, Me., and off Cape Ann, Mass., 25 fathoms.

Lafystius sturionis Kröyer.— Cape Ann, Mass., on cod.

Pontogeneia inermis (Kröyer).— Eastport, Me.

Dexamine thea Bœck.— Beverly Harbor, Mass., (J. H. Emerton, coll.).

Gammarus annulatus Smith.— Noank, Conn.

Mæra danæ (Stimpson).— Eastport, Me., and off Cape Ann, Mass.

Ischyrocercus anguipes Kröyer.— Eastport, Me., and Marblehead Neck, Mass., (J. H. Emerton coll.).

Ericthonius rubricornis (Stimpson).— Eastport, Me., and off Cape Ann, Mass.

Dulichia porrecta (Bate).— Eastport, Me.

Ægina longicornis spinossima Stimpson.— Salem, Mass.

Caprella linearis (Linné).— Annisquam, Mass.

Lepas anserifera Linné.— Portland, Me., from vessel.

Lepas fascicularis Ellis and Solander.— Eastport and Pemaquid, Me., Ipswich Bay and Lynn, Mass.

Lernæa branchialis Linné.— Annisquam, Mass.

Eubranchipus vernalis (Verrill).— Cohasset, Mass.

Joseph A. Cushman.

BOTANY.

Smith's Bacteria in Relation to Plant Diseases.[1]— Bacteriologists have long awaited Dr. Smith's work on the bacterial diseases of plants. We are now favored with the first part dealing with the methods of work and general literature of the subject. The monograph is not intended to take the place of the many text-books on the subject, but rather to supplement them. The work will be found useful to animal pathologists, as well as to plant pathologists. The monograph is the outgrowth of the work which has been carried on in the study of bacterial diseases of plants in the Laboratory of Plant Pathology, United States Department of Agriculture. The methods described have all been tested and are now in use in the Department. The following suggestions in regard to "A Study of an Organism" should be impressed on every beginner.

"Every one who has carefully inquired into the matter knows that the brief statement of the behaviour of an organism on nutrient agar, on gelatin, and on two or three other media, with perhaps a loose statement of its color and size, no longer constitutes a description which describes. Such accounts, of which there are a great many, usually fail to mention just those things which might serve to distinguish the organism from its fellows. If a new species is not to be described so that it can be identified by others, what then is the use of any name or description? The name will only serve to encumber future synonymy and to recall the incapacity of its author." The following opics indicate the broad and comprehensive scope of the subject matter: The Disease, The Organism, Physiology, Relation to Free Oxygen, Luminosity, Bibliography, General Literature, and Formulæ.

The author states that great stress should be laid on the minute morphology in a variety of cultures. He recommends especially the use of photography in microscopic work, which Dr. Koch has said "would certainly have prevented a great number of unripe pub-

[1] Smith, Erwin F. *Bacteria in Relation to Plant Diseases — Volume* 1, *Methods of Work and General Literature of Bacteriology exclusive of Plant Diseases.* Publication No. 27 Carnegie Institution of Washington, 285 pp., 31 pls., 146 text figs.

lications." Not only is it necessary to determine motility, but the organs of motility should be stained. The part of the work dealing with culture media is an excellent treatise; every working bacteriologist can get many valuable suggestions from it. The many conflicting statements as to the behavior of organisms by different authors arise largely from the character of the media used. In regard to vegetable media, he prefers to have them sterilized in the steamer rather than the autoclave. If boiling changes the nature of any fluids it is advisable to use the Chamberland or Berkefeld filter, but Chamberland bougies should not be used continuously for more than three days, because of the growth of small organisms in the walls of the filter, when they should be sterilized. There is a highly interesting discussion of sensitiveness to plant acids. The *Bacillus tracheiphilus* is used to show tolerance for sodium hydrate. Its tolerance for this substance can be considerably increased by inoculating each time from alkaline bouillons rather than from acid ones. The thermal relations of bacteria are among the most interesting and should be studied with great care. Under the head of economic aspects of the subject he argues with force that more attention should be given to the collection of accurate statistics by competent persons as an aid to legislature and governments. There are some excellent suggestions on natural methods of infection, how the parasites are introduced from one field to another by the roots of plants and in plants. The soil is a living thing and should not be transported from one field to another carelessly; the parasite may gain an entrance through wounds, by way of the stomata, lenticels, water pores, and nectaries. The keeping of records is an important part of the work of the experimenter, and it would be well for every bacteriologist to have Dr. Smith's work at hand and follow carefully the outlines given. The beginner should also be interested in the card-catalogue system used by the author.

The systematist will be interested in his discussion of nomenclature and classification, a subject naturally in a very chaotic state because systematic botanists have given so little attention to it, and medical men have cared even less about the classification of bacteria. He does not think it advisable to use Bacillus 1, 2, or 3 or A. B. C.; if the organism is really new and distinct, it should be given a name. Every working botanist will agree with him that all polynomials like *Bacillus coli-communis* are to be regarded as "*nomina excludenda.*" We agree also that all species antedating the Koch poured-plate method, which are not accurately described, should be abandoned.

"The *Micrococcus pellucidus*, although published quite recently and in the *Comptes Rendus* of the French Academy, is not described any better." "I find it quite impossible," says Mr. Stoddert, "to identify many species from published descriptions." Numerous complaints of this sort, made in recent years by well trained and competent men, sufficiently indicate the necessity of a thoroughgoing reform. He makes a plea for better and more careful descriptions, and concerning the use of the uncertain old names says: "And here I wish to register a protest against anything of this nature ever being done. If, in his own generation, a name cannot be associated beyond doubt with a particular organism by means of an author's description or figures or collected specimens, then this name should disappear, never to be revived. Societies of bacteriologists should unite in the near future on some authoritative date for the beginning of species priority, so that some sort of stability may be guaranteed to the nomenclature of the future."

In this part of the work there is a good discussion of the more modern systems of classification, that of Dr. Alfred Fischer, 1895, and the Migula classification, the latter of which is largely followed in this country. He then gives descriptions of the following orders and families: order Eubacteria, family Coccaceæ (Zopf emend.), Mig., family Bacteriaceæ, family Chlamydobacteriaceæ; order Thiobacteria, family Beggiatoaceæ, family Rhodobacteriaceæ, subfamily Thiocapsaceæ, subfamily Lamprocystaceæ, subfamily Thiopediaceæ, subfamily Amœbobacteriaceæ, subfamily Chromatiaceæ, to which he has very properly added the Myxobacteriaceæ. Some changes are proposed in nomenclature of genera and species. The genus Bacterium (Cohn) takes the place of Pseudomonas of Migula. The *Pseudomonas campestris* becomes *Bacterium campestris*. The *Bacillus anthracis* of Cohn is the type of a new genus, Aphlanobacter. The organism then should be called *Aphlanobacter anthracis* (Cohn) E. F. Smith. The genus Vibrio (Muller, Cohn) includes the *Spirillum cholera-asiaticæ*. Otherwise he follows the classification of Migula. There are good grounds for the changes here proposed.

The author has brought together formulæ for stains, synthetic and nonsynthetic culture media, tests for indol, and fixing fluids. Sixty-three pages are devoted to bibliography, well arranged and frequently provided with abstracts of the papers. Many excellent plates accompany the paper. The frontispiece contains halftones of five eminent bacteriologists: Ferdinand Cohn, Robert Koch, Louis Pasteur, Emile Roux, and Emile Duclaux.

This volume is the most important piece of general bacteriological literature that has been published in this country. It would be well indeed to have a copy of it in every working laboratory.

L. H. Pannuel

A Bibliographical Index of North American Fungi.[1]— For about thirty years Professor Farlow has been accumulating a card index referring to the fungi of North America. Nearly twenty years since, two authors' lists of works on this subject were published, and have been kept at the elbow of every student of our fungi since their appearance. The publication has now been commenced of the references to genera and species, as Publication No. 8 of the Carnegie Institution.

The preparation of an index may appear to the uninitiated a simple matter. A perusal of the author's seven-page preface is calculated to undeceive one who holds such an opinion, and the preface also contains some of the most sensible of recent commentary on nomenclature in natural history. A full list of abbreviations, and their consistent use, have rendered possible a wonderfully condensed presentation of the references to publications, which are kept within the limits of a single text line each. Synonyms are intelligibly collocated with accepted names, and free use is made of cross references.

In the preparation of the index, the author has had the assistance of Mr. Seymour's keen eyes for many years, and it may be predicted with safety that no important omissions will be found. Dr. Farlow's own familiarity with the literature of his subject is second to that of no one, and the knowledge of fungi that he has brought to the acceptance of admitted names, the placing of those treated as synonyms, and a very free critical annotation, is unequalled.

The Carnegie Institution is to be congratulated on having undertaken the publication of so generally useful a work as the *Index of North American Fungi*, the value of which in facilitating thoroughness of study is certain to make itself felt in all future publications on this important subject.

W. T.

Osterhout's Experiments with Plants.[2]—This book brings before

[1]Farlow, W. G. *Bibliographical Index of North American Fungi. Vol.* 1, *part* 1, "*Abrothallus*" *to* "*Badhamia*." The Carnegie Institution, Washington, Sept. 1, 1905. 8vo, xxxv + 312 pp.

[2]Osterhout, W. J. V. *Experiments with Plants.* New York, The Macmillan Company, 1905. 8vo, x + 492 pp., 252 figs.

the teacher and student the latest phase in the development of morphological conceptions. No longer is the plant treated as a mere mechanical complex of root, stem, and leaves. Instead it is presented as a living being, plastic in its environment. The work of root, stem and leaves, of the flowers and of the fruit, the influence of the surroundings upon the plant, are discussed in separate chapters, and these matters are made the subjects of extensive experimental investigation. Yet these experiments are simple in the extreme, as is the apparatus, in the construction of which a great deal of ingenuity has been displayed. It is such that any handy, intelligent boy can readily make it.

The primary-school teacher will find this book a valuable adjunct in her work; in the high school and university it can be given directly into the hands of the student, whom it forces to think rather than be content with the absorption of predigested statements.

The last two chapters, the one on plants which cause decay, fermentation, and disease and the other on making new kinds of plants, bring the laboratory more directly in touch with the outer world since they show how man can control diseases on the one hand and the formation of new varieties of fruits and flowers on the other. The introduction of a chapter relating chiefly to the work of Burbank and de Vries, with both of whom Dr. Osterhout is thoroughly acquainted personally, is a distinct innovation as far as botanical text-books are concerned. Then, too, the book deals with those other problems, which more recently have been suggested to the popular mind by newspaper and magazine articles, such problems as the pasteurizing of milk, vaccination and antitoxins, the self-purification of rivers and streams, nitrifying bacteria,— all of them issues of to-day and of great popular interest, interest which will necessarily extend to *Experiments with Plants*.

The book will prove equally acceptable from a purely botanical and from a purely pedagogical standpoint. It is intended to take the place of a similar book the writing of which was projected by Professor Bailey, to complete his series of Botanical Text-books. Certainly no one was better qualified to undertake the work than Dr. Osterhout, whose clear and concise manner of presenting the subject and whose easy, almost colloquial style make the book attractive.

The illustrations are as numerous as they are excellent. Most of them are from original photographs and drawings, a very pleasing feature, since it becomes tiresome to meet again and again the same familiar drawings, however excellent. The bookwork too, deserves

commendation. A fairly large type, good paper, and lack of typographical errors are always appreciated.

Hus

Sargent's Manual.[1]— No other person so well equipped for the description of North American trees as Professor Sargent could have been found, nor an illustrator so expert and practiced as Mr. Faxon; hence it results that no manual of our trees so good as the present could have been expected from any other source. To the makeup of the book the Riverside Press have brought their usual skill. The total result, therefore, is a well devised, well written, well illustrated, and well made book, condensing into convenient size what is necessary for the study of our trees, and yet not skimping the descriptions. As was to be expected, the sequence (after Engler and Prantl) and nomenclature (after Sargent's Silva) are rather radically modern, while the treatment of species is rather conservative except in the daily amplifying genus Cratægus, to which further species are here added.

A synopsis of families with a key based on their leaves renders the first placing of a given form easy, while genera and species are differentiated in the same manner.

If any fault is to be found with the book it will probably be with the absence of synonymy, especially that referring to the new names introduced, except for references to differing names employed in the author's *Silva.*

W. T.

Notes.— Contributions from the Gray Herbarium of Harvard University, n. s., no. 31, published as vol. 41, no. 9, of *Proceedings of the American Academy of Arts and Sciences* under date of July 24, contains "Descriptions of Spermatophytes from the Southwestern United States, Mexico, and Central America," by Greenman, and "Diagnoses and Notes relating to American Eupatoriæ," by Robinson.

A reprint of the original edition of Nuttall's *Journal of Travels into the Arkansas Territory, during the Year* 1819, Philadelphia, 1821, forms vol. 13 of Thwaites' *Early Western Travels,* in course of publi-

[1] Sargent, C. S. *Manual of the Trees of North America exclusive of Mexico.* Boston and New York, Houghton, Mifflin and Co., 1905. 8vo, xxiii + 826 pp., 644 text figs.; with map showing the principal tree regions of the United States.

cation by the Arthur H. Clark Company of Cleveland. The editor's preface to the present volume contains an interesting sketch of Nuttall's work.

The 3-volume edition of James' *Account of an Expedition from Pittsburgh to the Rocky Mountains, performed in the Years* 1819, 1820 .... *under the command of Maj. S. H. Long*, London, 1823, forms volumes 14–17 inclusive of Thwaites' *Early Western Travels.*

The third series of *Vegetationsbilder*, by Karsten and Schenck (Jena, Fischer, 1905) presents, thus far, "Flower Gardens of Brazilian Ants," by Ule, "Vegetation of Russian Turkestan," by E. A. Bessey, and the "Vegetation of Java," by Büsgen, Jensen, and Busse.

Professor Peck's "Report of the State Botanist, 1904" forms *Bulletin* 94 (*Botany* 8) *of the New York State Museum*, and bears date July, 1905.

Coste's *Flore descriptive et illustrée de la France* reaches Orchidaceæ in the recently issued fourth fascicle of vol. 3.

Vol. 4, part 3, of Wood's *Natal Plants*, issued in June, contains plates 351–375, with descriptive text.

A revised classification of roses, by Baker, is published in the *Journal of the Linnean Society — Botany*, of July 1.

Miss Eastwood has published a very usable handbook of the trees of California under date of July 8 as *Occasional Papers no.* 9 *of the California Academy of Sciences.* Leaf, fruit, and general character keys make the paper useful, and it is illustrated by 57 plates, partly from nature but largely after drawings by the late Dr. Kellogg.

A revision of Berberis is being published by Schneider in the *Bulletin de l'Herbier Boissier.*

The species of Cratægus of Berks Co., Pa., are considered by C. L. Gruber, of Kutztown, Pa., in three pamphlets, the first two of which were issued by the Berks County Natural Science Club in 1903, while the last appears in the *Bulletin of the Torrey Botanical Club* for 1905.

L. A. Dode has recently issued from vol. 18 of the *Mémoires de la Société d'Histoire Naturelle d'Autun* a monographic account of Populus.

A note on his American observations on the *biennis* group of Œnothera is separately printed by DeVries from the *Album der Natuur.*

Beccari's long-interrupted palm studies have been resumed, and he has recently published several important papers in *Webbia,* issued by Count Martelli of Florence.

Habit photograms of *Sabal palmetto* are given by Nehrling in *Die Gartenwelt* of July 15.

A note on some agaves flowering at Le Martola is published by Berger in *The Gardeners' Chronicle* of August 26.

From tests recorded in *Bulletin no. 72 Bureau of Plant Industry, U. S. Department of Agriculture,* Scofield concludes that the salt water limit of *Zizania aquatica* is approximately represented by 0.03 of the normal solution of sodium chloride,— when the water is not appreciably salty to the taste.

An illustrated paper on the ancestors of the "Big Trees" (Sequoia), by Berry, appears in *Popular Science Monthly* for September.

According to vol. 5, no. 3, of the *Bulletin du Jardin Impériale Botanique de St. Pétersbourg,* the St. Petersburg garden has recently secured three specimens of *Osmunda regalis* over 1000 years old.

Two fascicles (222 and 223) of Engler and Prantl's *Die natürlichen Pflanzenfamilien,* by Brotherus, dealing with mosses, have recently been issued.

A lecture on diatoms with illustrations, by Mann, is contained in vol. 48, part 1, of *Smithsonian Miscellaneous Collections.*

Regeneration among kelps is considered by Setchell in vol. 2, no. 5, of *University of California Publications — Botany.*

A well illustrated popular account of desert plants is published by Holder in *The Country Calendar* of August.

A paper on the megaspore membrane of the gymnosperms, by Thomson, forms no. 4 of the *University of Toronto Studies, Biological Series.*

Karyokinetic papers of importance occupy vol. 24, part 1, of the *Jahrbücher fur wissenschaftliche Botanik,* issued in July.

The importance of investigations of seedling stages, as presented by Dr. Harris before the St. Louis Congress of 1904, is analyzed in *Science* of August 11.

A paper on seed studies made by Todaro at the Modena agricultural station is published in *Le Stazioni Sperimentali Agrarie Italiane*, vol. 38, fascicle 5–6, with a colored plate showing the tests of dry and viable seeds of Trifolium and Hedysarum.

A paper on the dispersal of seeds by wind is published by Ridley in the *Annals of Botany* for July.

The pollination of *Cypripedium spectabile* by honey-bees is described and photographically illustrated by W. H. Sargent in *Country Life in America* for September.

A paper on the insect galls of Indiana, by M. T. Cook, is published in the *29th Annual Report of the Indiana Department of Geology and Natural Resources.*

A paper on "The Science of Plant Pathology" is published by Stevens in *Popular Science Monthly* for September.

Hedgcock, in *Science* of July 28, reports some of the results of his work with "crown gall" of fruit trees, walnuts, etc.

Some vine diseases in Sonoma County, Cal., are discussed by Butler in *Bulletin no.* 168 *of the Agricultural Experiment Station of the University of California.*

A report on plant diseases of the State, by Sheldon, forms *Bulletin no.* 96 *of the West Virginia Agricultural Experiment Station*, issued on June 30.

A second Hemileia, on orchids, is described and figured by Massee in *The Gardeners' Chronicle* of August 19.

A paper on white rust of the lemon is published by Cavara and Mollica in vol. 17 of the *Atti della Accademia Gioenia di Catania.*

Three new fungi from Catalina Island are described by Ellis and Everhart in the April *Bulletin of the Southern California Academy of Sciences*, which also contains a short article by Blanche Trask on San Jacinto plants.

Nigrosphæria is the name given by Gardner to a new genus proposed for *Sphæria* (*Hypocrea*) *setchellii* Harkness, in vol. 2, no. 6, of *University of California Publications — Botany.*

Thaxter publishes "Preliminary Diagnoses of New Species of Laboulbeniaceæ — VI" as Contributions from the Cryptogamic Lab-

oratory of Harvard University — LXII, in vol. 41, no. 11, of *Proceedings of the American Academy of Arts and Sciences,* issued in July.

Mangin and Viala give an account of *Stearophora radicicola,* a fungus parasite of the roots of Vitis, in the *Revue de Viticulture* of July 6.

Holway has begun the publication of a series of descriptions with photomicrographic illustrations of the North American Uredineæ. The first fascicle, dealing with the Puccinias of Ranunculaceæ, Berberidaceæ, Papaveraceæ, Bromeliaceæ, Commelinaceæ, Juncaceæ, Liliaceæ, Amaryllidaceæ, Iridaceæ, and Orchidaceæ, was issued on the 15th of April.

A paper by Peglian on the Urophlyctis disease of alfalfa is published in vol. 14, no. 12, of *Atti della R. Accademia dei Lincei.*

An illustrated account of the Ustilagineæ of Connecticut, by Clinton, forms *Bulletin no.* 5 *of the Geological and Natural History Survey* of that State.

An illustrated article on "Mushrooms and Toadstools" is published by Arthur in *The Country Calendar* for September.

A well illustrated preliminary report on the Hymeniales of Connecticut, by White, forms *Bulletin no.* 3 *of the Geological and Natural History Survey* of the State.

An illustrated account of new Citrus creations of the Department, by Webber and Swingle, is separately printed from the *Yearbook of the United States Department of Agriculture for* 1904.

The maple-sugar industry forms the subject of *Bulletin no.* 59 *of the Bureau of Forestry, United States Department of Agriculture,* by Fox and Hubbard.

A paper on red gum (Liquidambar), by Chittenden and Hatt, has recently appeared as *Bulletin no.* 58 *of the Bureau of Forestry, United States Department of Agriculture.*

De Vries describes some of Burbank's methods in *Popular Science Monthly* for August.

An account of Kola in Yoruba Land is given by Bernegau in *Der Tropenpflanzer* for July.

Statistics concerning yerba maté (*Ilex paraguayensis*) are given in *Daily Consular Report No.* 2247, of May 2.

An account of rubber cultivation in Hawaii is given by Smith in *Press Bulletin no.* 13 *of the Hawaii Agricultural Experiment Station,* dated July 20, 1905.

An article on gutta percha, with photograms of Palaquium, is published by Murdoch in *The Indian Forester* of June.

An exhaustive account of the aboriginal use of wood in New York is given by Beauchamp in *Bulletin* 89 (*Archeology* 11) *of the New York State Museum.*

Preliminary accounts of the recent International Botanical Congress at Vienna are given by Rendle in *The Journal of Botany* for July 1 and Britton in *Science* of August 18.

Under the title *Webbia,* Count Martelli has recently issued a volume of botanical papers, by various writers, commemorative of the 50th anniversary of the death of Barker-Webb.

An appreciative sketch of Delpino, by Ludwig, is published in *Naturwissenschaftliche Rundschau* of August 10.

The Journals.— *Botanical Gazette,* July:— Smith, "Undescribed Plants from Guatemala and other Central American Republics — XXVII"; Snow, "The Development of Root Hairs"; Frye and Blodgett, "A Contribution to the Life History of *Apocynum androsæmifolium*"; Nelson, "Contributions from the Rocky Mountain Herbarium — VI"; B[arnes], "The Vienna Congress"; and Florence Lyon, "Another Seed-like Character of Selaginella."

Botanical Gazette, August:— Moore, "Sporogenesis in Pallavicinia"; McCallum, "Regeneration in Plants — I"; Dean, "On Proteolytic Enzymes — II"; Schneider, "Contributions to the Biology of Rhizobia — IV, Two Coast Rhizobia of Vancouver Island, B. C."; Beal, "The Vitality of Seeds"; Rose and Painter, "Some Mexican Species of Cracca, Parosela, and Meibomia"; Greenman, "A New Krynitzkia."

The Bryologist, September:— Chamberlain, "Maryland Bryophytes and Two Mosses from Virginia"; Williams, "Notes on Luzon Mosses"; Holzinger, "*Bryum fosteri*"; Britton, "The Botanical Congress at Vienna"; Sargent, "Lichenology for Beginners — III"; Fink, "What to Note in the Macroscopic Study of Lichens — II"; Gilbert, "The Advantage of Frequent Visits to Moss Localities."

Bulletin of the Torrey Botanical Club, July:— Latham, "Stimulation of Sterigmatocystis by Chloroform"; Murrill, "The Polyporaceæ of North America—XI, a Synopsis of the Brown Pileate Species"; House, "Further Notes on the Orchids of Central New York"; Piper, "The two Eastern Species of Melica"; Gruber, "Cratægus in Berks County, Pennsylvania — III."

Bulletin of the Torrey Botanical Club, August:— Cannon, "On the Transpiration of *Fouquieria splendens*"; Martin, "Studies on the Effect of some Concentrated Solutions on the Osmotic Activity of Plants"; Schneider, "*Chroolepus aureus* a Lichen"; Piper, "*Poa gracillima* Vasey and its Allies."

A small quarterly of miscellaneous contents, has been started by T. J. Fitzpatrick of Iowa City under the title *The Iowa Naturalist.*

Journal of Mycology, May:— Morgan, "A New Chætosphæria"; Lawrence, "Notes on the Erysiphaceæ of Washington"; Ellis and Bartholomew, "Two New Haplosporellas"; Beardslee, "The Rosy-spored Agarics or Rhodosporæ"; Ricker, "Notes on Fungi — II, with New Species from Various Localities"; Bates, "Rust Notes for 1904"; Thom, "Some Suggestions from the Study of Dairy Fungi"; Kellerman, "Index to North American Mycology"; Kellerman, "Notes from Mycological Literature — XV."

Journal of the New York Botanical Garden, August:— MacDougal, "The Suwarro, or Tree Cactus."

Pittonia, part 28:— Greene, "Revision of Eschscholtzia"; "A New Papaveraceous Genus [Petromecon]"; "A Study of Dendromecon"; "Suggestions Regarding Sanguinaria."

The Plant World, June: — Ramaley, "A Botanist's Trip to Java"; Spillman, "Cactus as a Forage Plant."

The Plant World, July:— Reed, "A Brief History of Ecological Work in Botany"; Blodgett, "Fasciation in Field Peas."

Proceedings of the Iowa Academy of Sciences for 1904:— Shimek, "Botany in its Relation to Good Citizenship"; Fink, "Notes on American Cladonias"; Fink, "Some Notes on Certain Iowa Algæ"; Macbride, "The Slime Moulds of New Mexico"; Gow, "An Ecological Study of the Sabine and Neches Valleys, Texas"; Fawcett, "Variation in Ray Flowers of *Anthemis cotula* and other Composites"; Buchanan, "Notes on a Thermophilic Bacillus"; Pammel, "Notes

on the Flora, especially the Forest Flora, of the Bitter Root Mountains"; Seaver, "An Annotated List of Iowa Discomycetes"; Rueda, "The Biology of the *Bacillus violaceus laurentius* or *Pseudomonas janthina*"; Anderson, "Plants New to the Flora of Decatur County, Iowa"; Lindly, "Flowering Plants of Henry County"; Watt, "Growth and Pigment Production of *Pseudomonas janthina*"; Peck, "The Flowering Plants of Hardin County."

Proceedings of the Society for the Promotion of Agricultural Science, 26:— Bailey, "What is Horticulture?"; Lazenly, "The Economic Uses of Wood"; Pammel, "Some Fungus Diseases Common in Iowa During the Season of 1904"; Beal, "The Vitality of Seeds"; Arthur, "The Part taken by Teleutospores and Æcidia in the Distribution of Maize and Cereal Rusts."

Rhodora, August:— Shear, "Letter of Dr. Asa Gray to Lewis D. de Schweinitz"; Blanchard, "The Yellow-fruited Variety of the Black Raspberry"; Fernald, "The Genus Arnica in Northeastern America," "*Spergula sativa* in Connecticut," "Some Lithological Variations of Ribes," and "*Anaphalis margaritacea* var. *occidentalis* in Eastern America"; Ballard, "A Second Vt. Station for *Arenaria macrophylla*."

Torreya, July:— Schneider, "An Example of Complex Life-relationship"; Christ, "Quelques mots sur l'article de Mr. Underwood 'A much Named Fern'"; Greene, "Derivation of the Name Chamæcrista"; Harper, "Two Misinterpreted Species of Xyris."

Torreya, August:— Coker, "Observations on the Flora of the Isle of Palms, Charleston, S. C."; Cockerell, "Names of Insects"; Hanmer, "A Note regarding the Discharge of Spores of *Pleurotus ostreatus*."

GEOLOGY.

Notes.— *Water Supply and Irrigation Papers*, 97, 98, 99, *and* 100, form the report of the branch of the Division of Hydrography dealing with stream measurements for the year 1903. These four reports represent over fifteen hundred pages of valuable data, collected from almost all the important streams of the United States. The results have been compiled by J. C. Hoyt, under the direction of F. H. Newell.

The relation between rainfall and run-off, under different climatic conditions, is very clearly brought out in many of the tables.

The "Report of Progress of Stream Measurements for the Calendar Year 1904" forms *Water Supply and Irrigation Papers* 124–135 inclusive. The various portions of the country are treated in the separate bulletins, as follows:—

124, Pt. 1, Atlantic Coast and New England Drainage.
125, " 2, Hudson, Passaic, and Delaware River Drainages.
126, " 3, Susquehanna, Patapsco, Potomac, James, Roanoke, Cape Fear, and Yadkin River Drainages.
127, Pt. 4, Santee, Savannah, Ogeechee, and Altamana Rivers, and Eastern Gulf of Mexico Drainage.
128, Pt. 5, Eastern Mississippi River Drainage.
129, " 6, Great Lakes and St. Lawrence River Drainage.
130, " 7, Hudson Bay, Minnesota, Wapsipinicon, Iowa, Des Moines, and Missouri River Drainages.
131, Pt. 8, Platte, Kansas, Meramee, Arkansas, and Red River Drainages.
132, Pt. 9, Western Gulf of Mexico and Rio Grande Drainages.
133, " 10, Colorado River and the Great Basin Drainages.
134, " 11, The Great Basin and Pacific Ocean Drainage in California.
135, Pt. 12, Columbia River and Puget Sound Drainages.

A new term applying to veins, namely "rift-veins," is proposed by J. A. Reid, in a paper entitled "The Structure and Genesis of the Comstock Lode" (*University of California, Bulletin of the Department of Geology*, vol. 4, no. 10, pp. 177–199). The type of this kind of vein is the Comstock, where "the surface 'east vein,' the famous bonanza, and the 'vein' now being worked have an identical origin. Their formation lies in the fact that the lower part of the hanging wall block has settled more than the upper, relative to the foot wall, and has been torn apart by the stresses developed."

The *Journal of Geology* for July–August, 1905, contains the following articles: "The Geographical Cycle in an Arid Climate," by W. M. Davis; "Notes on Baked Clays and Natural Slags in Eastern Wyoming," by E. S. Bastin; "The Delaware Limestone," by C. S. Prosser; "*Megacerops tyleri*, a New Species of Titanothere from the Bad Lands of South Dakota," by R. S. Lull; "Comment on the 'Report of the Special Committee on the Lake Superior Region,'" by A. C. Lane.

"The Lead, Zinc and Fluospar Deposits of Western Kentucky," by E. O. Ulrich and W. S. T. Smith, forms *Professional Paper* no. 36 of the United States Geological Survey. The general geology of the district is treated by Ulrich, while the detailed description of the different deposits is by Smith. Smith regards the fluorite as having been deposited from circulating underground waters, and having been derived, probably, from the limestones of the region. On noticing the number of faults and dikes that have been mapped in this region, one questions why a deep-seated source of the fluorite is regarded untenable.

The character of the triclinic feldspars at high temperatures has recently been investigated by Messrs. Day and Allen. The careful measurements of the melting points, points of crystallization, specific gravities, etc., all prove that in triclinic feldspars, isomorphism is complete. The slides prepared from the various feldspar mixtures were examined by J. P. Iddings, and he found that, optically, the feldspars correspond very closely to the mixtures prepared. The optical portion of the paper is illustrated by six remarkably clear plates. This report is entitled "The Isomorphism and Thermal Properties of the Feldspars," and is published by the Carnegie Institution of Washington, as *Publication* no. 31.

An exhaustive description of the Bingham District of Utah has been prepared by Boutwell, Keith, and Emmons. This report, which is published as *Professional Paper* no. 38 of the United States Geological Survey, consists of four parts. The first part is a general presentation of the problem by Emmons. The second part is by Keith, and treats the areal geology of the region. The third, and by far the most important portion of the monograph, is by Boutwell. The successive stages of oxydation are well shown by the fact that in the surface zone free gold, some oxides, and carbonates were found; on descending, a zone of carbonates occurred, with a little sulphide; while, at a greater depth, the sulphides became more and more abundant until the carbonate and oxide ores have given place almost entirely to sulphides, of which the copper sulphide is most important, economically. The fourth portion of the report is an appendix describing the fossils of the Bingham District, by Girty.

Professional Paper no. 34 of the United States Geological Survey, "The Delavan Lobe of the Lake Michigan Glacier of the Wisconsin Stage of Glaciation and Associated Phenomena," by W. C. Alden,

is a detailed study of southern Wisconsin and northern Illinois. The report is fully illustrated by maps, representing the successive stages in the deglaciation of the district.

Publication 101 of the Field Columbian Museum, entitled "The Rodeo Meteorite" by O. C. Farrington, is a description of a medium octahedrite with high phosphorus content, weighing about one hundred pounds. The mass was found in 1852, in the State of Durango, Mexico.

A series of experiments which aim to give some quantitative values for the pressures exerted by growing crystals, has been performed by G. F. Becker and A. L. Day. In these experiments, it has been proved that crystals increase most rapidly on their under surfaces, and thus lift the earlier formed portions. So energetic is this action that a kilogram weight was raised several millimeters by an alum crystal whose bearing surface was only a small fraction of a square centimeter. The force, therefore, is believed to be of the same order of magnitude as the resistance that crystals offer to crushing. The published account of these experiments appears in the *Proceedings of the Washington Academy of Sciences*, vol. 7, pp. 283–288.

P. S. S.

(*No. 469 was issued January 20, 1906*)